THE ECOLOGY OF THE MANX SHEARWATER *PUFFINUS PUFFINUS* ON RHUM, WEST SCOTLAND

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"There is a great deal of stormy magnificence about the lofty cliffs, as there is generally round the shores of Rum; and they are, in most places, as abrupt as they are inaccessible from the sea. The interior is one heap of rude mountains, scarcely possessing an acre of level land. It is the wildest and most repulsive of all the islands. The outlines of Halival and Haskeval are indeed elegant, and render the island a beautiful and striking object from the sea. If it is not always bad weather in Rum, it cannot be good very often."

M^{ac}Culloch, 1824.

"Yet the birds which hover so closely over the bosom of the deep at times ascend in the air to an elevation of many hundred feet as, for example, when the individuals which nest in the interior of Rum return to their well-nigh inaccessible burrows among the mountain crags of that island deer-forest."

H.A. M^{ac}Pherson, 1898.

ACKNOWLEDGEMENTS

I was first introduced to Manx shearwaters by Neville McKee and I thank him for encouraging my interest in seabirds.

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Most of all, I thank my husband, Dann Hale, for unstinting help in the field, for pancake breakfasts after long nights out on the hill, and for his endless patience, support and encouragement through it all.

CANDIDATE'S DECLARATION

I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is of my own composition. No part of this work has been submitted for any other degree.

Kate Thompson

Kate Thompson

CONTENTS

ABSTRACT

The aim of this project was to investigate the ecology of Manx shearwaters on Rhum, with particular emphasis on the influence of predation and other extrinsic factors upon breeeding success and population dynamics.

Brown rats were not found to be active predators of shearwaters on Rhum. Few rats were present in the shearwater colony during the birds' breeding season, but larger numbers scavenged on the remains of shearwater eggs and chicks during the autumn and early winter. Rats are apparently prevented from becoming established in the shearwater colony by food shortage in late winter and by the colony's location within Rhum. Golden eagles, peregrine falcons and great black-backed gulls do prey upon shearwaters on Rhum but have an insignificant effect upon the shearwater population.

Hatching success in the colony varies markedly from year to year and is significantly negatively correlated with the incidence of heavy rain during the incubation period. This arises from the variation in susceptibility to flooding among nesting burrows. The tendency for individual burrows to flood was quantified and was found to have a significant influence upon the probability of successful breeding.

Weights at fledging showed a significant seasonal decline, apparently due to increased difficulty for adults in provisioning chicks late in the season. Heavy fledglings are apparently more likely to survive than light ones so that there is selective advantage in breeding as early as possible. The ultimate and proximate control of timing of laying is discussed.

There was evidence of year to year variation in feeding conditions around the colony. Chicks grew more slowly in 1985 than in 1984 and were fed less frequently.

The implications of these findings to the population dynamics and conservation of the colony are discussed.

Chapter 1

INTRODUCTION

Taxonomy of the Manx Shearwater

The Manx shearwater is one of 19 species of shearwaters included in the family Procellariidae to which the fulmars, prions and gadfly petrels also belong. The family is one of four in the order Procellariiformes or Tubinares in which are also included the albatrosses, Diomedeidae; the storm petrels, Hydrobatidae; and the diving petrels, Pelecanoididae (Nelson, 1980). The shearwaters are typically pelagic, spending most of their lives at sea and only coming to land in order to breed. The long, narrow wings, compact plumage and webbed feet of these birds are well adapted to long flights at sea, and pursuit of the fish and cephalopods upon which they feed.

Distribution of the Manx Shearwater

Murphy (1952) recognised 8 sub-species of the Manx shearwater distributed from Australasia, Hawaii and the west coasts of Central and North America to the Mediterranean and North Atlantic. Unless otherwise stated, all future references to shearwaters in this thesis refer to the nominate race of the Manx shearwater Puffinus puffinus puffinus. This form of the Manx shearwater breeds throughout the north-east Atlantic from Madeira, the Desertas and Azores to the coasts of Brittany and the British Isles, and further north, in the Faroes and Iceland (Harrison, 1982; Pasquet 1981). The Manx shearwater has been regularly seen in the summer months along the eastern seaboard of North America from New York to Newfoundland since the early 1950s (Post, 1967). Most of these birds appear to be pre-breeders from the north-east Atlantic colonies but within the past 15 years

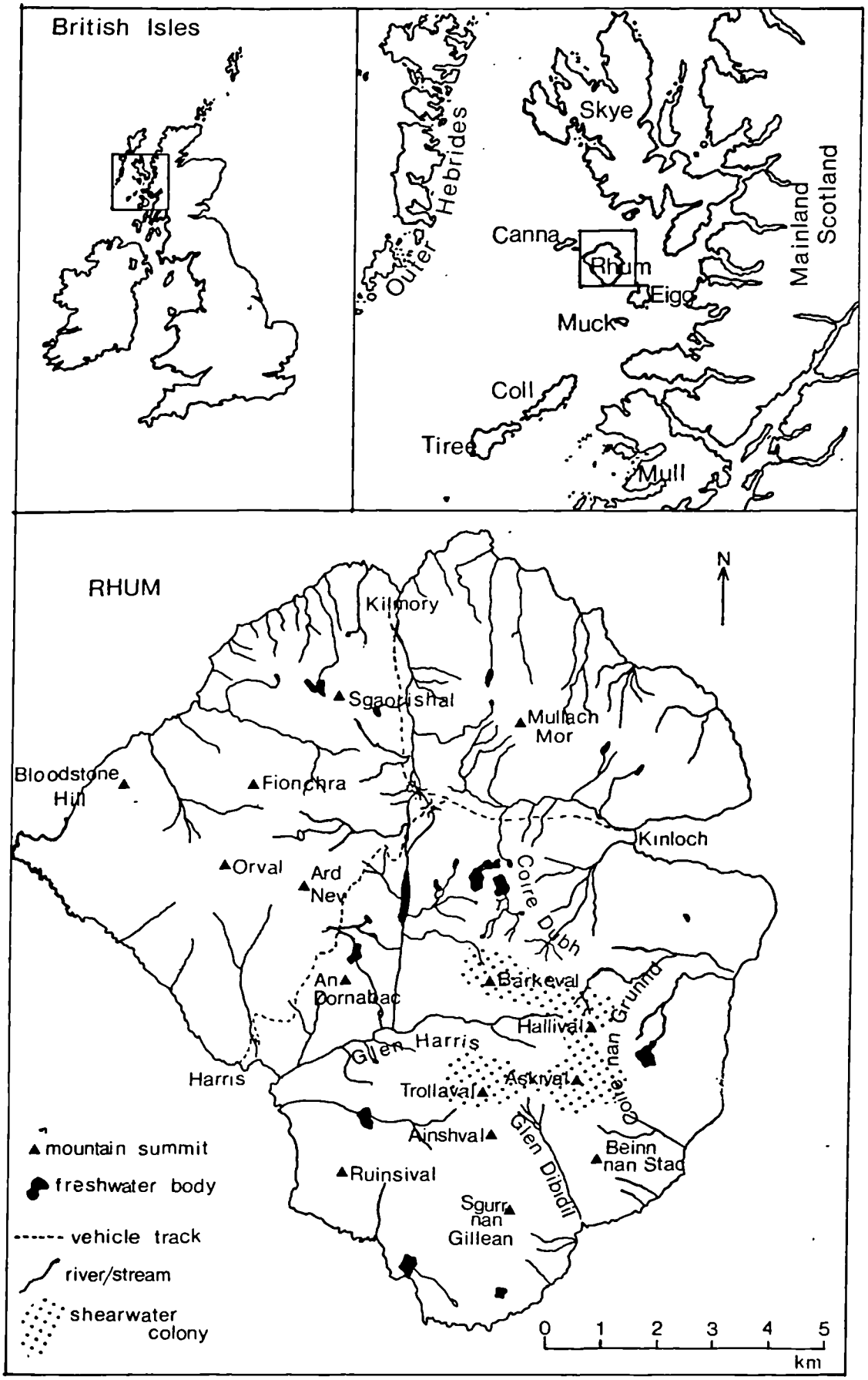
new colonies have been developing on islands off the coasts of Massachussetts and Newfoundland (Bierregaard et al., 1975; Lien and Grimmer, 1978).

Around the coasts of the British Isles there are three main breeding centres, namely on islands off south-west Ireland; in the Irish sea where the islands of Skokholm and Skomer off Pembrokeshire together provide breeding grounds for ca. 130,000 pairs (Perrins, 1967; Corkhill, 1973); and in the Hebrides. Within the Hebrides the Manx shearwater is most numerous on the Small Isles of the Inner Hebrides with smaller colonies in the St. Kilda group, the Treshnish Isles and on Bearasay, Lewis (Bourne and Harris, 1979; Robson and Wills, 1963). In the past, Manx shearwaters were apparently more common in the Outer Isles, and on Mingulay they formed part of the crofters' rent until displaced by puffins some time around 1800 (Elwes, 1869). Currently the largest single colony of this species occurs on the island of Rhum (Fig. 1) where Wormell (1976) estimated there to be a total of 116,000 ± 19,000 occupied burrows. There are smaller colonies on the neighbouring islands of Eigg, Canna and Muck (Thom, 1986).

The Breeding Cycle

Following the pioneering work of Lockley in the 1930s, there has been extensive study of the breeding biology of the Manx shearwater on Skokholm and the following brief summary is based on Harris (1966b). The Manx shearwater is typical of its genus in having a protracted breeding season and low annual reproductive output. Breeding birds return to the coasts of Britain in February and March to prepare their burrows and build up body reserves before egg laying which peaks in the second week of May following a 10 to 14 day long pre-laying exodus or "honeymoon" period. Incubation of the single egg is shared by both parents over a period of about 51 days in shifts averaging 6 days at a time. Re-laying within one season is extremely rare but may occur where the original egg is damaged shortly after laying. The downy

Fig 1·1 LOCATION OF THE STUDY AREA



chicks are brooded continuously for a few days but thereafter are visited and fed only at night. The chicks are fed by both parents and reach a peak weight of about one and a half times the adult weight at approximately 50 days after hatching. Thereafter, until fledging at around 70 days of age, the chicks lose weight as the parents provide less food. Most of the young fledge during September and migrate immediately to their wintering grounds off the east coast of South America. Birds do not return to their natal colony in their first year but in subsequent summers spend progressively more time at the colony until their first breeding attempt when five or more years old. Estimates of adult survival rates from ringing recoveries indicate an average adult expectation of life of up to 29 years (Harris, 1966a).

The Study Area

The island of Rhum (Fig 1) is situated some 24 km due west of the town of Mallaig on the north-west coast of Scotland, and has an area of almost 10,700 hectares. Most of the island is mountainous and very rugged. In the past there were settlements at several points around the coast, but currently only the village of Kinloch on the east of the island is occupied with a total population of around 30 people. Since 1957 Rhum has been a National Nature Reserve owned and managed by the Nature Conservancy Council (N.C.C.).

The shearwater colony is situated on the slopes of the mountain ridge in the south-east part of the island from an altitude of around 350m to the summits. Most of the burrows are on Barkeval (584m), Hallival (717m), Askival (807m), and Trollval (702m). These mountains form part of the remains of a Tertiary volcano and are composed of complex strata of ultra-basic and basic rocks. The soils derived from these rocks are sandy and nutrient-deficient so that only certain heathland and arctic-alpine species are able to colonize the exposed terraces. However, within the

shearwater colony the birds' nutrient-rich droppings have allowed a rich Agrostis-Festuca grassland and stable soils to develop (Wormell, 1976). This effect makes the main concentrations of nesting burrows stand out as vivid "greens" on the otherwise drab hillsides.

History of Shearwaters on Rhum

In the absence of early written references to Rhum, it is impossible to ascertain when the island was first colonised by shearwaters. However the name Trollval - mountain of the trolls - suggests that shearwaters were present when the Vikings named the mountain in the 11th century. Similar names, Trøllanes and Trøllhøvdi, persist in the Faeroes where shearwaters still breed today (Williamson, 1973). There is a written Norse reference to the Calf of Man colony dating from 1014 but the name "Manx" was not applied to these birds until 1676 (Williamson, 1940).

When Dean Munro visited Rhum in the first half of the 16th century he referred to there being "mony solenne geese" (Munro, 1549) by which he may have meant shearwaters as Rhum does not have suitable nest sites for gannets to which the name solan geese is normally applied (Nelson, 1978). No reference is made to shearwaters in a report made on the island around 1580 (Skene, 1880) but Martin Martin refers specifically to them at the turn of the 18th century (Martin, 1716).

In the first detailed account of the economy and agriculture of Rhum, written in 1772, there is no reference to the harvesting of shearwaters for their down and oil as was common in other colonies eg. the Isle of Man (Williamson, 1940). In contrast to Mingulay (see above) the tenants' rents on Rhum were paid in cash (Pennant, 1774). However Gray (1871) states that "in earlier times the breeding place was on the coast, and the birds were then collected at the close of the season, as at Barra, and salted for winter use."

The first truly scientific account of the island dates from 1764 when John Walker noted "the Puffin of the Isle of Man [ie. Manx shearwater] builds here ....it keeps the sea all year round except in hatching time. It builds in holes underground and we found its nests among loose rocks above a mile from the shore." The Victorian successors to this early naturalist were well aware of the importance of the Rhum shearwater colony and from 1870 there are numerous accounts of shearwaters in the Small Isles (M^{ac}Pherson, 1888; Harvie-Brown and Buckley, 1892).

Past and Present Shearwater Research on Rhum

When Rhum was declared a National Nature Reserve in 1957, the first Chief Warden, Peter Wormell, began research on the Rhum shearwater colony. From 1958 to 1973 the breeding success of between 20 and 30 individually marked pairs of shearwaters in observation burrows on the north east face of Hallival was monitored each year. In addition to these birds and their chicks, up to 540 adults and 240 fledglings were ringed annually (N.C.C. records, unpublished). Between 1965 and 1969, Wormell also made the first census of the shearwater colony. The total area of the colony was estimated by summing the areas of all the "greens" discernable from aerial photographs. In addition the densities of occupied burrows within these "greens" were calculated from counts of burrows in a series of random 0.04 hectare plots. The summed products of the estimated colony area and average occupied burrow density for each major part of the colony gave a figure of 116,000 $\pm$ 19,000 for the total number of occupied burrows (Wormell, 1976).

From 1973 until the start of the current research, further work on the colony was restricted to updating the original colony size estimate and unsystematic ringing of adults caught on the surface of the colony at night. New counts of occupied burrow densities in random plots on Trollval and Hallival in 1978 and 1979 suggested increases of

27% and 25% respectively on these mountains since Wormell's census. However, due largely to the wide variation in burrow densities recorded in different plots, the apparent increase was not statistically significant (Thompson and Thompson, 1980). The next census in 1982, in which occupied burrow densities were calculated from counts in 58 random 225m^2 plots placed throughout the colony, suggested a significant decrease in colony size of 32% since Wormell's census (Philips, 1982). It is, in fact, extremely difficult to detect real population trends when different random plots are examined by different observers at various times of year. Also, in the absence of any revised estimate of the physical extent of the colony all these censuses have assumed it to be identical to the original which was itself based on photographs taken in 1946. In the past two years a series of permanent plots have been established to allow occupied burrow densities to be monitored more systematically in future and updated mapping of the "greens" from the ground has begun (Furness and Thompson, with fieldwork assistance from "Earthwatch" volunteers). Preliminary results from that work suggest that the occupied colony area has not changed greatly over the past 40 years.

The current study was undertaken as a result of the N.C.C.'s concern about the possible impact of brown rats on the Rhum shearwater colony. This concern arose in view of the conservation significance of the Rhum colony, and as a result of reported reductions in the extent of neighbouring colonies on Eigg and Canna, possibly attributable to rat predation (Evans and Flower, 1967). In addition to assessing the impact of brown rats, and other predators, upon the Rhum colony (Chp. 6), I examined the effects of nest site selection and timing of breeding on breeding success (Chps. 3 and 4). Diet, and chick growth, feeding frequency and food conversion efficiency were also studied (Chp. 5) as were the biometrics and seasonal pattern of weight change of adults (Chp. 2). Thus, the main aim of this study has been to

investigate the influence of extrinsic ecological factors such as predators, food, habitat and climate on the breeding biology and population dynamics of the Rhum shearwater population (Chp. 7). Detailed studies of the Manx shearwater population on Skokholm, and in particular that of Brooke (1977), provided a baseline with which to compare the Rhum birds.

Any attempt to unravel the complex web of factors which may influence shearwater breeding success, is limited by the inability to sex birds other than those identified as members of known pairs during the egg laying period (Serventy, 1956). Additional limitations in studying the Rhum colony stemmed from its relative inaccessibility, the rugged terrain and wet climate. It proved impossible to age any of the individual birds examined in the course of this study as only a very small proportion of currently breeding birds were ringed as fledglings. As age has been demonstrated to influence several of the parameters important in determining individuals' breeding success (Brooke, 1977) this has been a major drawback in this instance.

Methods

Much of the information presented in the following chapters was derived from monitoring breeding activity in 100 breeding burrows on the north-east face of Hallival. This part of the colony was selected for study due to its relative ease of access from Kinloch and because much of the past ringing activity was concentrated in that area. These observation burrows were created in April 1984 by removing a small plug of soil from above the nest chamber and replacing it with a rock or a wire basket filled with the original soil to form a light-tight removable "lid". Further details of methods used are given in the appropriate chapters.

Statistical analyses follow Campbell (1979) and the SPSS statistical package (Nie et al, 1975).

Nomenclature

The scientific names of species mentioned in the text are given in Appendix 2. Throughout this thesis I use the modern spelling of Rhum as this is currently used on Ordnance Survey maps. In fact, the correct Gaelic or Norse name is Rum (Love, 1983).

Chapter 2

BIOMETRICS OF MANX SHEARWATERS ON RHUM

Introduction

In this chapter I present data on the weights and measurements of Manx shearwaters from the Rhum colony. Male and female dimensions are compared with each other and with those of Manx shearwaters from Skokholm. Changes in average weights over the breeding season are also discussed.

Methods

The body measurements taken in the field were as follows:-

Wing length:- the distance from the foremost extremity of the carpus to the tip of the longest primary feather, estimated to the nearest mm by flattening and straightening the wing along a stopped rule; known as maximum cord (B.T.O., 1972).

Bill length:- the distance from the limit of feathering to the most distant part of the curve of the hook, estimated to the nearest 0.1mm using vernier calipers.

Head and bill length:- the distance from the back of the skull to the most distant part of the curve of the hook of the bill, estimated to the nearest mm on a rule with one fixed and one sliding stop.

Tarsus length:- the distance from the distal end of the tarso-metatarsus to the middle of the mid-tarsal joint, estimated to the nearest 0.1mm with vernier calipers.

Weight:- estimated to the nearest 5g using a 1000g Pesola or Salter spring balance.

All weights and measurements were taken by the author to eliminate inter-observer variation.

For comparison of male with female measurements birds were categorised as females only if they were found to have a bluish, distended cloaca during the laying period (Serventy, 1956). Similarly, birds were only classed as known males if they were mated with a female identified as above.

Results

Comparison of male and female dimensions

The mean wing lengths, bill lengths, head and bill lengths and tarsus lengths of known males and females are given and compared in Table 2.1. It can be seen that on Rhum male Manx shearwaters are significantly larger than females over all the body dimensions measured. A discriminant function for distinguishing between males and females on the basis of head and bill length and the ratio of wing to bill length is shown in Fig. 2.1. This function was derived by the S.P.S.S. discriminant function programme as the best two-variable function obtainable from the available body dimensions plus their ratios. This function correctly classifies 76.7% of the known sex birds used in its derivation.

Table 2.1 Mean body dimensions in mm (± S.E.) of male and female Manx shearwaters breeding on Rhum. Sample size for females is 61 and for males 55.

	Male	Female	p (t-test)
Wing length	242.8 ± 0.57	240.3 ± 0.55	<0.01
Bill length	35.24 ± 0.182	34.41 ± 0.188	<0.01
Head & bill length	82.7 ± 0.22	80.5 ± 0.25	<0.001
Tarsus length	46.18 ± 0.134	45.61 ± 0.157	<0.01

Fig. 2·1 DISCRIMINANT FUNCTION SEPARATING MALES AND FEMALES ON THE BASIS OF BODY DIMENSIONS.

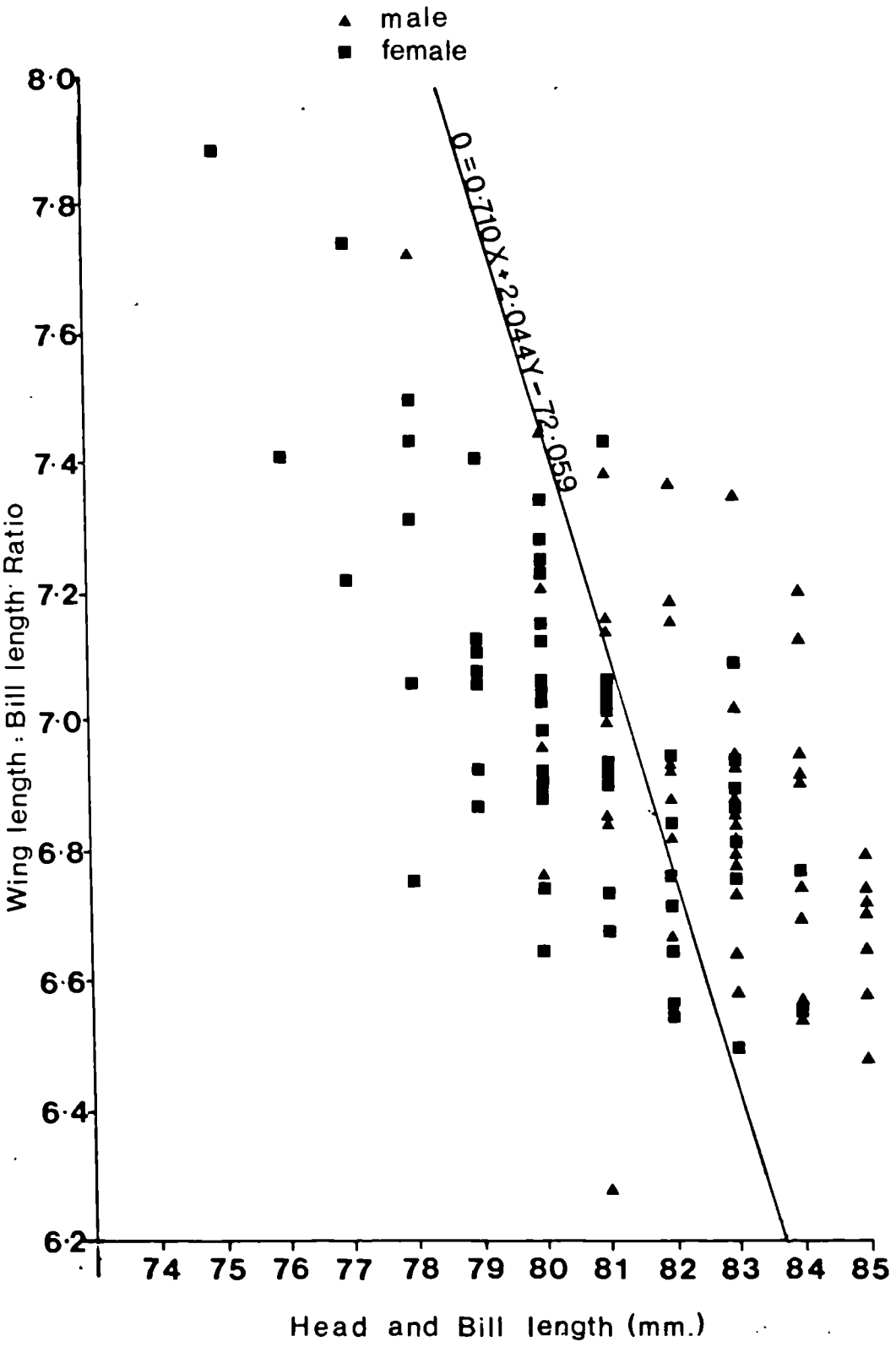


Table 2.2 compares wing, bill and tarsus lengths of birds of each sex on Rhum with those of breeding birds on Skokholm (Brooke, 1977). Rhum males have significantly longer wings and tarsi than those from Skokholm but the difference in bill length is not significant. By contrast only the tarsus length of females on Rhum is significantly greater than that of their Skokholm counterparts.

Table 2.2a Mean body dimensions in mm (± S.E.) of male Manx shearwaters breeding on Skokholm (Brooke, 1977) and Rhum (this study). Sample size for Rhum is 55 and for Skokholm 47.

	Rhum	Skokholm	p (t-test)
Wing length	242.8 ± 0.57	240.1 ± 0.74	<0.01
Bill length	35.24 ± 0.182	34.95 ± 0.206	N.S.
Tarsus length	46.18 ± 0.134	45.73 ± 0.141	<0.05

Table 2.2b Mean body dimensions in mm (± S.E.) of female Manx shearwaters breeding on Rhum (this study) and Skokholm (Brooke, 1977). Sample size for Rhum is 61 and for Skokholm 47 except for tarsus where N = 46.

	Rhum	Skokholm	p (t-test)
Wing length	240.3 ± 0.55	240.6 ± 0.64	N.S.
Bill length	34.41 ± 0.188	34.13 ± 0.165	N.S.
Tarsus length	45.61 ± 0.157	44.65 ± 0.182	<0.001

Seasonal changes in weight

Mean monthly weights of successful and unsuccessful breeders of each sex were calculated in 1984 and 1985 by averaging all the individual weights recorded in each category in each month. In this instance successful breeders were defined as those birds which fledged chicks while unsuccessful breeders were paired birds which produced eggs but failed to fledge chicks. These data (± 95% confidence intervals) are presented in Fig. 2.2. Table 2.3 presents the same information together with the results of t-test comparisons between sexes and months in each year for both successful and unsuccessful birds.

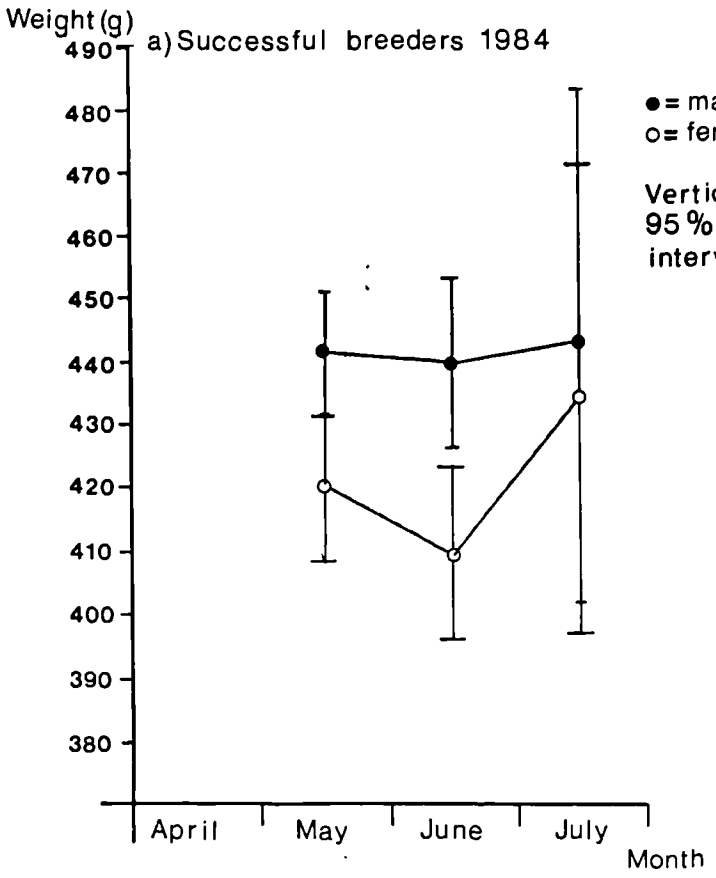
The main features of these results are as follows:-

(1) Male shearwaters on Rhum were generally heavier than females throughout the 1984 and 1985 breeding seasons. This is to be expected in view of the greater size of male birds over all the body dimensions measured.

(2) Paired males increased in weight from the prelaying period in April to the laying and early incubation period in May, in both 1984 and 1985. Unsuccessful breeding females in 1984 also increased significantly in weight from April to May, but in 1985 females showed no significant change in weight over the same months.

(3) Birds of both sexes which successfully incubated their eggs and reared chicks maintained a fairly constant average weight from May to July during the 1984 breeding season. During this period there were marked day to day changes in individual's weights as birds lose on average $10.9 g day^{-1}$ (n = 117, S.E. = 0.356) during incubation shifts, and during chick rearing commonly bring feeds of 70g to their offspring (Chapter 5). By comparison, unsuccessful breeders which failed to hatch their eggs but which revisited their burrows during the 1984 breeding season declined in weight from June

Fig. 2·2 SEASONAL WEIGHT CHANGES OF ADULTS FROM OBSERVATION BURROWS



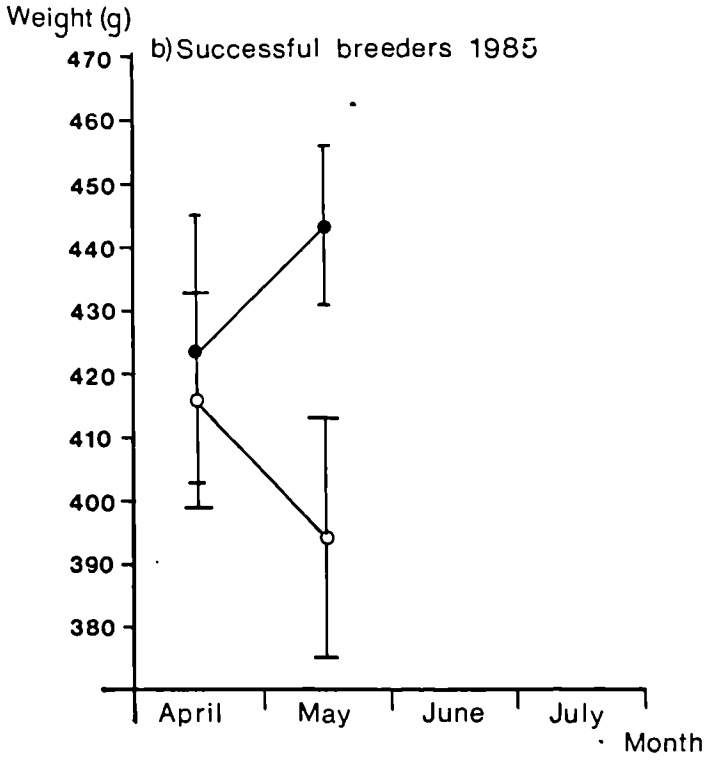
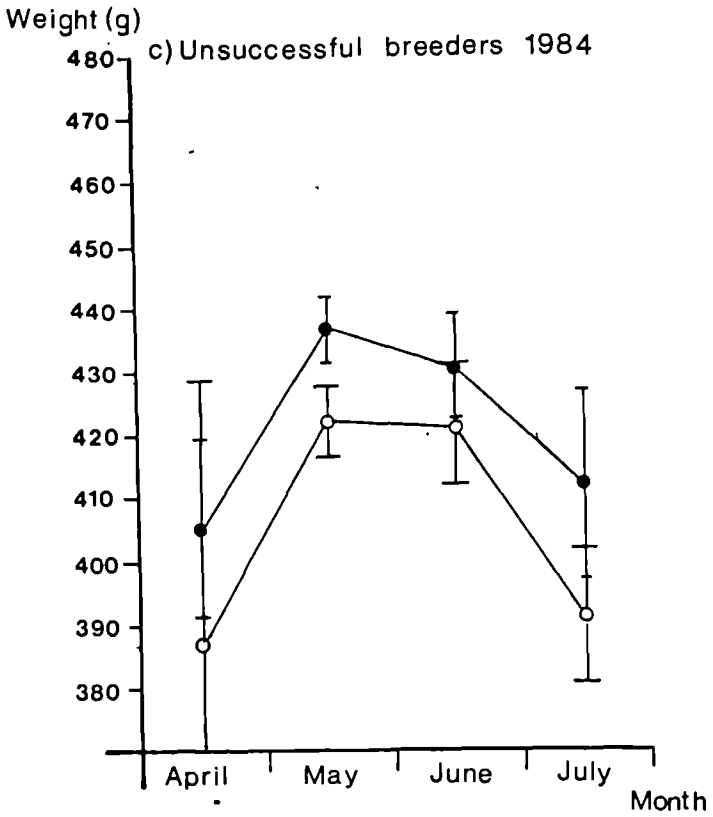
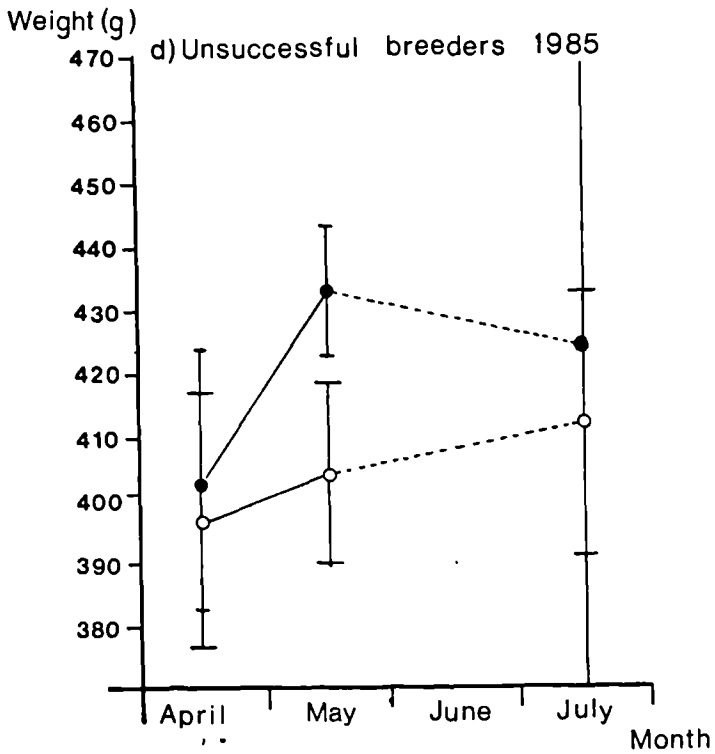


Fig. 2·2 cont.


Weight (g)
c) Unsuccessful breeders 1984
480
470
460
450
440
430
420
410
400
390
380
April
May
June
July
Month


Weight (g)
d) Unsuccessful breeders 1985
470
460
450
440
430
420
410
400
390
380
April
May
June
July
Month

to July. Insufficient data were available to examine seasonal changes in weight after May in 1985.

Table 2.3a Mean monthly weights in grammes (± S.E.) of successful breeders in 1984. Sample sizes in parenthesis.

	p months	Males	p sexes	Females	p months
April		-		-	
	N.S.				N.S.
May		441.4 ± 4.93 (46)	< 0.01	420.1 ± 5.50 (34)	
	N.S.				N.S.
June		439.8 ± 6.56 (21)	< 0.01	409.8 ± 6.45 (20)	
	N.S.				N.S.
July		443.0 ± 14.71 (5)	N.S.	434.4 ± 15.74 (8)	

Table 2.3b Mean monthly weights in grammes (± S.E.) of successful breeders in 1985. Sample sizes in parenthesis.

	p months	Males	p sexes	Females	p months
April		424.0 ± 9.39 (10)	N.S.	416.0 ± 7.52 (10)	
	N.S.				N.S.
May		443.5 ± 6.23 (33)	< 0.001	394.2 ± 9.01 (18)	
June		-		-	
July		-		-	

Table 2.3c Mean monthly weights in grammes (± S.E.) of unsuccessful breeders in 1984. Sample sizes in parenthesis.

	p months	Males	p sexes	Females	p months
April		405.5 ± 6.27 (11)	N.S.	386.3 ± 13.44 (4)	
	< 0.01				< 0.05
May		437.0 ± 2.69 (174)	< 0.001	422.2 ± 2.92 (108)	
	N.S.				N.S.
June		430.9 ± 4.12 (55)	N.S.	421.5 ± 4.85 (64)	
	< 0.05				< 0.01
July		412.1 ± 6.97 (14)	< 0.05	391.1 ± 4.62 (9)	

Table 2.3d Mean monthly weights in grammes (± S.E.) of unsuccessful breeders in 1985. Sample sizes in parenthesis.

	p months	Males	p sexes	Females	p months
April		403.1 ± 8.76 (8)	N.S.	396.7 ± 8.86 (9)	
	< 0.05				N.S.
May		433.2 ± 5.12 (52)	< 0.01	404.1 ± 7.01 (27)	
	N.S.				N.S.
June		408.3 ± 17.64 (3)	N.S.	373.3 ± 7.27 (3)	
	N.S.				N.S.
July		423.8 ± 21.93 (4)	N.S.	412.0 ± 9.23 (10)	

Pre-laying weights on Rhum and Skokholm

As illustrated in Table 2.4, mean weights of both male and female paired birds during the pre-laying period were higher on Skokholm in 1974 than on Rhum in 1985 despite the greater size of the Rhum birds (cf. Table 2.2).

Table 2.4 Mean weights in grammes (± S.E.) of paired birds during the pre-laying period on Skokholm in 1974 (Brooke, 1978c) and on Rhum in 1985 (this study). Sample sizes are shown in parenthesis.

	Skokholm 1974 (March - April)	Significance (t-test)	Rhum 1985 (April)
Males	456.4 ± 4.43 (32)	$p < 0.001$	414.7 ± 6.81 (18)
Females	427.3 ± 8.29 (15)	$p < 0.05$	406.8 ± 6.05 (19)

Discussion

Size difference between the sexes

My observations support those reported in Cramp and Simmons (1977) that male Manx shearwaters have longer wings and tarsi than females. On Skokholm, Brooke (1978c) found bill and tarsus lengths to be greater in males but he did not find any difference in wing length. On Rhum, male Manx shearwaters have been found to have longer wings than those from Skokholm while the females do not vary and this may explain the apparent anomaly in size differences between the sexes observed at the two colonies. On Rhum, the most useful single dimension measured for discriminating between males and females was head length. This dimension has been found useful for sexing other species of seabirds including puffins and kittiwakes (Barrett et al., 1985) and gulls (Coulson et al., 1983). As it is impossible to sex shearwaters by

plumage or when observed at sea, there is no information that could be used to test the possibility that the sexes are adapted to exploit rather different feeding niches. Another possible evolutionary explanation for the greater size of males might lie in their role in procuring and guarding nest burrows. In order successfully to defend its burrow a male should spend as much time as possible ashore guarding the burrow against intruders. As basal metabolic rate (B.M.R.) increases with weight (W) such that:-

$$B.M.R. \propto W^{y} \quad \text{where } y < 1$$

it follows that larger birds take a longer period of time to use up the same percentage by weight of body reserves than do smaller ones. In the wandering albatross, which exhibits more extreme sexual dimorphism, it has been found that males on average incubate the egg for over half of the incubation period without sustaining any greater percentage loss of body weight than their smaller mates (Croxall and Ricketts, 1983). The greater size of male Manx shearwaters might therefore represent a compromise between an optimum for the exploitation of a particular feeding niche and the reproductive necessity of retaining possession of a suitable nest site. Greater size might also benefit males in direct conflicts with other males over burrow ownership.

Differences in body dimensions between Skokholm and Rhum

It appears that male shearwaters on Rhum are larger than their Welsh conspecifics. This tendency for birds of the same species to be larger at greater latitudes has been observed in several species; eg. the northern race of the herring gull, Larus argentatus argentatus, is bigger than the more southern L. a. argentaeus (Cramp and Simmons, 1983) and both subspecies further exhibit clinal increases in body size with latitude (Monaghan et al., 1983). Similarly, in Norway both kittiwakes and puffins show increases in body dimensions with colony latitude (Barrett et al., 1985). In contrast to

the size difference in males, that between females from the two colonies is much less pronounced. This situation might arise as a result of the observed tendency for females to disperse from their natal colonies, in contrast with the extreme natal site faithfulness found in males (Brooke, 1978b). To date there have been few records of birds from the Irish Sea colonies being found in the Hebrides, although in 1973 a 1 year old bird from Copeland (Co. Down) and a 5 year old from Skokholm were controlled on Canna (Ramsey, 1974). The size of the Rhum colony combined with the lack of regular monitoring serve to minimise the chances of any ringed birds from other sites being discovered, so that the extent of interchange between the Irish Sea and Hebridean colonies is at present unknown.

Seasonal changes in weight

My observations of month to month changes in weight differ from those of Brooke (1978c) for Skokholm. There, birds of all age classes showed a peak weight in the prelaying period of March and April and thereafter lost weight to reach a minimum but fairly constant weight between May and July. There was a tendency to gain weight again in August. Brooke suggests that this pattern arises from the movement of good feeding grounds closer to the breeding colony during the incubation and early chick stages. Such improved feeding conditions should enable birds to fly between the colony and feeding grounds and fulfil their breeding requirements on lower body reserves than at the beginning of the season when feeding grounds are more distant. The increase in weight in August is to be anticipated for birds about to embark on a long migration. This theory is supported by ringing recoveries which have shown birds from Skokholm to travel as far south as the Bay of Biscay to feed in the pre-laying period but to feed closer to the colony thereafter (Perrins and Brooke, 1976).

There are no ringing records to indicate the location of the Rhum shearwaters' feeding grounds through the season. However, if a similar situation as described for Skokholm were to apply to Rhum, the observed increase in weight in May from the prelaying period would be unexpected and might indeed be taken to suggest that the feeding grounds of the Rhum shearwaters become more distant from the colony as the breeding season progresses, which seems unlikely. A more plausible explanation may be that the Rhum birds exploit the same feeding areas throughout the breeding season and increase in weight in May as food availability in these areas improves. That the Rhum birds may suffer a relative food shortage at the start of the breeding season is supported by the greater weights of paired birds on Skokholm during the pre-laying period despite the larger size of the Rhum birds. Another difference between the Skokholm and Rhum birds, which might also suggest the absence of good feeding areas within the Hebridean area during the early part of the season, is that whereas the Pembrokeshire colonies are first revisited in late February/early March (Lockley, 1942) shearwaters are not found returning to Rhum until the middle of March (N.C.C. records, unpublished; pers. obs.). These arguments assume that body reserves reflect the ease with which birds can find food, so that low reserves are due to relative food shortage. Another possible hypothesis is that birds maintain a weight that is "optimal"; ie. that they carry reserves in anticipation of foraging difficulties and shed these surplus reserves when they are no longer likely to be needed. If this were the case, the lower weights of Rhum birds during the pre-laying period would imply the existence of a richer and more predictable food supply than that available to the Skokholm birds. In view of the apparent difficulties experienced by the Rhum birds in accumulating sufficient reserves for egg laying in some years (Chp. 4) this seems unlikely to be the case. A brief review of the oceanographic

difference in feeding ecology of the Rhum and Skokholm birds appears to be reflected in the observed patterns of seasonal weight changes at the two colonies. The lower pre-laying weights of the Rhum shearwaters may reflect difficult feeding conditions prior to the establishment of local summer frontal systems.

Chapter 3

BREEDING SUCCESS AND BURROW QUALITY

Introduction

The nocturnal and burrow-nesting habits of Manx shearwaters at their breeding grounds have apparently evolved in response to avian predation pressure on these relatively small and, on land, clumsy birds. In addition to minimising the risk of predation of adults during incubation, nesting in burrows also frees both parents to forage simultaneously when feeding chicks. This may be vital to successful fledging in situations where food supplies are scarce or unpredictable in location.

In this chapter I examine some implications of burrow-nesting for the Manx shearwater on Rhum, and in particular the direct influence which choice of burrow exerts upon probable breeding success. Some indirect effects arising from the characteristics of individual birds in relation to their burrows are also discussed.

Methods

Breeding success data were obtained through regular checking of the observation burrows described in Chapter 1. In this way information was obtained on numbers of eggs laid, chicks hatched and chicks surviving to fledge. In 1984, the burrows were checked frequently during incubation to obtain information on the duration of incubation shifts. In order to assess the impact of disturbance caused by such checks, the burrows were divided into three equal groups. Burrows in group A were checked, where possible, on every second day, those in group B were checked on one day in four, while the

group C burrows were checked only once in eight days. In 1985 and 1986 observation burrows were not reopened after laying until either chick calls were heard in response to a playback recording of adult shearwater calls, or 51 days had elapsed.

In order to examine the influence of burrow characteristics upon breeding success, the following parameters were measured for each observation burrow:-

1) Ground slope immediately over the nest chamber:- measured to the nearest degree using a clinometer.

2) Overall hill slope over 10m centered on the burrow:- measured to the nearest degree using the clinometer sighted from one pole to a second of the same height 10m uphill from the first.

3) Burrow length:- measured to the nearest 0.05m off a flexible cable inserted into the nest chamber from the main burrow entrance.

4) Burrow curvature:- calculated as the shortest distance (to the nearest 0.05m) between the entrance and nest chamber, measured above ground, divided by the actual burrow length. Thus a completely straight burrow would have a curvature of 1, while a burrow in which the tunnel curved back towards the entrance would have a curvature approaching 0.

5) Depth of soil above the nest chamber:- measured to the nearest cm.

6) Nearest neighbour distance:- measured to the nearest 0.05m from the main entrance of the burrow to the closest entrance of any other burrow.

7) Number of other burrows with entrances lying within a 1m radius of the burrow's main entrance.

8) Proportion of the burrow lying under rock:- given by the length of the burrow tunnel roofed by rock expressed as a percentage of the total length.

9) Total number of entrances to the burrow.

10) Aspect of the main entrance:- recorded to the nearest eighth compass point ie. N., N.E., E. etc.

11) Area of the main entrance:- calculated as maximum height x maximum breadth, each measured to nearest cm.

In order to compare burrow densities in different habitats, fifty points on the north-east face of Hallival were randomly picked from a photograph of the area. In July and August 1984 these points were located on the ground by reference to the numerous boulders present. At each point the number of shearwater burrows within a plot of 3m radius were counted and the substrate/vegetation cover recorded.

The impact of rainfall upon breeding success was examined using mean annual hatching and fledging success data from study burrows on Rhum and Canna over the 28 year period from 1958 to 1985. The data for Rhum were from Wormell (N.C.C., unpublished records) and this study, while the Canna data were provided by R. L. Swann. The incubation period was taken as extending from 23rd April, one week prior to the earliest laying date observed in my observation burrows, to the 27th July which was the hatching date of the last egg laid in these burrows in 1985. This should include the incubation period of the majority of the eggs from which the hatching rate figures were derived. The chick rearing period was taken as extending from 12th June, the date on which an egg laid on 23rd April would be expected to hatch, to 5th October, the date on which a chick hatched on 27th July would be expected to fledge. The rainfall data used were daily records from the Kinloch meteorological station on Rhum over the years for which shearwater breeding success data were available. In addition, for comparison of rainfall amounts within the study area with those recorded in Kinloch, a monthly raingauge was sited at about 530m up the north-east face of Hallival in March 1985. This was subsequently read on the first day of each month.

On the night of 22-23 July 1986, I measured bill lengths, head and bill lengths, wing lengths, tarsus lengths, and weights of 104 adult shearwaters caught on the ground on Hallival. I repeated this with 115 birds on 28-29 July and

R.W. Furness took the same measurements of 101 birds on 29-30 July. These data were used to investigate correlations between body dimensions and weight, in order to assess condition. The measurement of a large sample of birds in one night was designed as a control of the seasonal fluctuations in adult weights observed at the colony (cf. Chapter 2). All measurements of shearwaters were taken as described in Chapter 2.

Results

Burrow Density in Relation to Habitat Type.

Table 3.1 shows the average densities of burrows in different habitat types on Hallival, as assessed from the random 3m radius plots described above. These data indicate that while burrow densities within the "greens" are greater than elsewhere, there is great variation in burrow densities over small areas in all habitats. Nevertheless, the difference in mean burrow density between the two major habitat types, namely "green" and boulder field, is significant (Fisher-Behrens test, $d = 6.668$, $p < 0.01$).

Breeding Success

The numbers of eggs laid, chicks hatched and chicks fledged in the observation burrows in 1984, 1985 and 1986 are shown in Table 3.2. The consistently high fledging success is in accordance with previous studies of Manx shearwaters (Harris, 1966b; Perrins et al., 1973; Brooke, 1978a; R. Swann, pers. comm.; Wormell, N.C.C. records unpublished)

Table 3.1 Burrow densities in relation to habitat type on the north-east face of Hallival.

Habitat type	No. of plots	Mean burrow density per m^2 (± S.D.)
"Green" ie nutrient - rich moss-grass sward.	16	0.338 (± 0.176)
Border of "green" with boulder or scree slope	6	0.189 (± 0.191)
Boulder field	13	0.038 (± 0.034)
Scree slope	6	0.047 (± 0.076)
Nutrient-poor grass slope	6	0.029 (± 0.057)
Earth banks	3	0.130 (± 0.054)

Table 3.2 Breeding success in observation burrows on Rhum, 1984-1986.

	1984	1985	1986
No. of accessible burrows	89	92	92
No. of eggs laid	73	48	36
No. of eggs hatched	19	25	27
% of eggs hatched	26.0	52.1	75.0
No. of chicks fledged	16	21	23*
% of chicks fledged	84.2	84.0	85.2?

*:- chicks still alive on 1st September 1986

Hatching success in the observation burrows in 1984 was not representative of the colony as a whole, because many of the eggs were deserted due to the disturbance caused to incubating birds when checking adult identity. The sensitivity of the birds to disturbance at this time is illustrated by Table 3.3 which shows a Chi^2 analysis of desertion in relation to checking frequency. Hatching success was significantly reduced in those burrows checked most frequently. The adults appeared particularly sensitive to disturbance during the first half of the normal incubation period. Reduction in breeding success due to interference in the course of research is often mentioned but seldom quantified. Boersma and Wheelwright (1979) found that daily checks of fork-tailed storm petrel burrows reduced hatching success to 58% as compared with 84% in control burrows checked only four times in the latter part of the incubation period. Serventy and Curry (1984) concluded that repeated disturbance of a small short-tailed shearwater colony over the course of a 30 year study, had contributed to the colony's decline.

Table 3.3 Egg desertion in relation to checking frequency during incubation, 1984

(O=observed frequencies)
(E=expected frequencies)

	Checking Frequency		
	Low ie < 25% days	High ie ≥ 25% days	
Egg success			
Abandoned within 25 days	O = 3 E = 7.9	O = 15 E = 10.1	18
Abandoned after more than 25 days	O = 15 E = 13.2	O = 15 E = 16.8	30
Hatched	O = 12 E = 8.8	O = 8 E = 11.2	20
Total	30	38	68

$\chi^2 = 7.93$, d.f. = 2, $p < 0.05$.

In 1985 and 1986 observation burrows were not opened during the incubation period, so that the hatching success rates recorded are probably representative of the colony as a whole. Unlike fledging success, hatching success of Manx shearwaters has been found to vary considerably from year to year. Over 14 years of monitoring ca.30 observation burrows on Rhum, Wormell found hatching success to vary from 48% to 100% (N.C.C., unpublished records). On Canna hatching success in a sample of ca. 40 burrows has ranged from 42% to 87% over 10 years (R. Swann, pers. comm.), while in the course of Brooke's (1977) 4 year study on Skokholm, hatching success in ca. 70 burrows varied from 64% to 81%.

Such year to year variation in hatching success could arise from feeding conditions in some years being more favourable than in others, thus making it easier for breeding adults to synchronise incubation shifts correctly. However, on Rhum there is evidence that weather conditions, and particularly rainfall, play a direct role in determining hatching success in the colony. Rhum's location and topography are responsible for a wet climate with an average annual rainfall at Kinloch of 2373mm (N.C.C., 1974). The amounts of rain-water collected in the gauge on Hallival confirm that rainfall in the shearwater colony is even greater than that recorded at sea level (Table 3.4).

Table 3.4 Summer monthly rainfall amounts (mm) in Kinloch and on Hallival, 1985 and 1986.

	1985		1986	
	Kinloch	Hallival	Kinloch	Hallival
April	241	290	219	242
May	122	138	340	495
June	75	163	81	141
July	268	-	160	365
August	441	711	146	196
September	320	587	-	-

In 1985, Rhum experienced the wettest summer recorded in the 27 years over which meteorological records have been kept. During this period I observed flooding of burrows and found instances of eggs having been washed out of burrows. Figure 3.1 illustrates average hatching success in observation burrows on Rhum and Canna in relation to the percentage of days over the incubation period on which rainfall amounts at Kinloch exceeded twice the 1958 to 1972 daily average for the given month. For Rhum the correlation coefficient, r, is -0.5225 (n = 15, $p < 0.02$) and for Canna -0.6489 (n = 12, $p < 0.01$). If the data for both islands are combined, the correlation coefficient is -0.5759 (n = 27, $p < 0.001$). Hatching success also tends to decrease with total rainfall during the same period but the relationship is less marked (Rhum, r = -0.3335, N.S.; Canna, r = -0.4864, p = 0.05; combined, r = -0.4031, $p < 0.02$). Thus it seems that the distribution of rainfall, and in particular the incidence of unusually heavy rain, has a greater influence on colony hatching success than total rainfall per se.

Unlike hatching success, fledging success showed no significant correlation with rainfall amounts or distribution during the chick rearing period for either or both islands. This probably arises from the tendency for rainfall during the chick period to be correlated with that during incubation as shown in Table 3.5. Thus years which are wet during the chick period may generally also have been wet during incubation, so that those pairs in burrows susceptible to flooding are likely to fail in their breeding attempt before their egg hatches. The lack of any correlation between fledging success and rainfall also tends to confirm the supposition that the influence of rainfall on hatching success is a direct physical effect, and not the indirect result of some unknown influence of rainfall on food availability.

Fig 3·1 HATCHING SUCCESS IN RELATION TO RAINFALL DURING INCUBATION

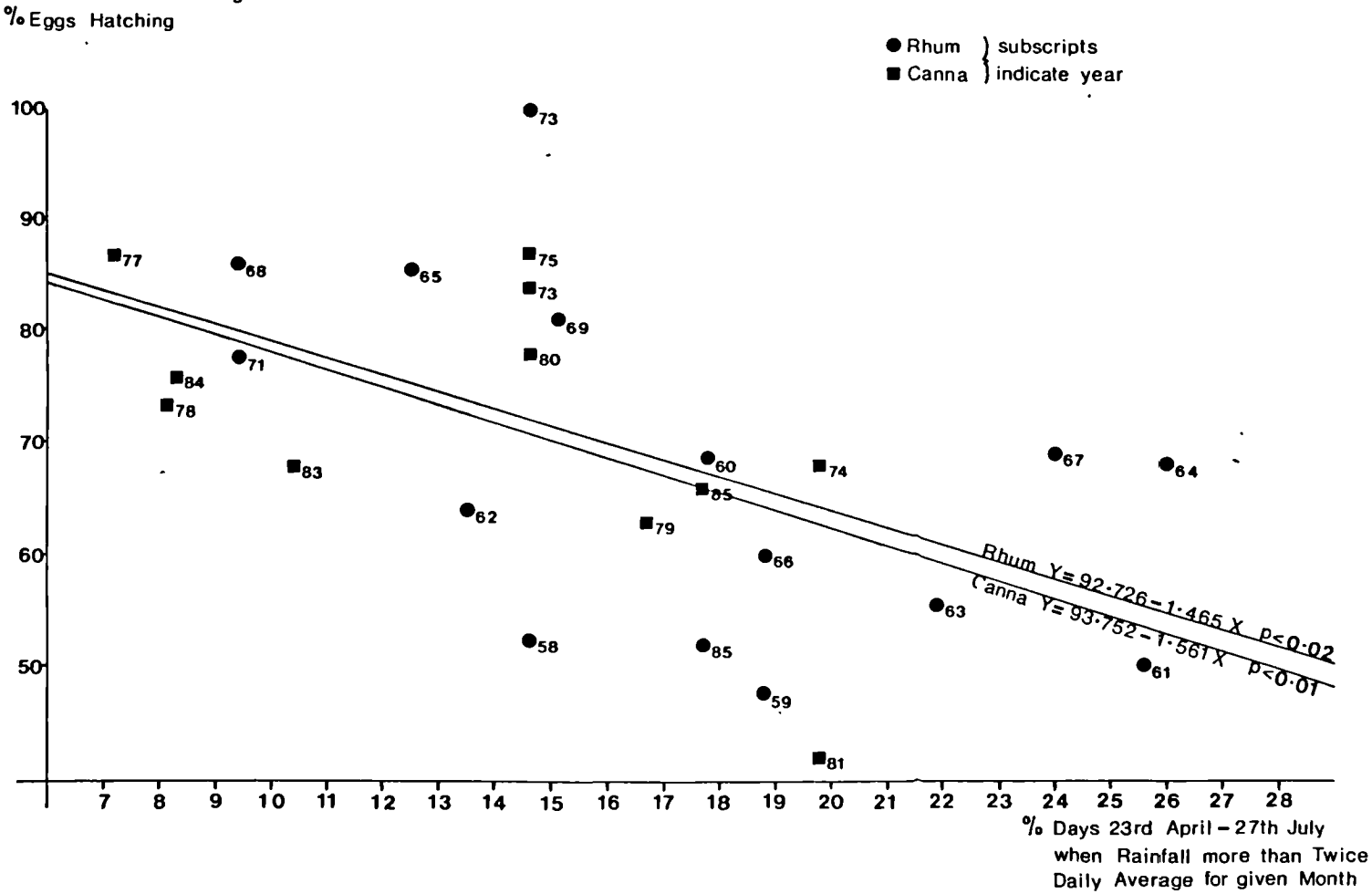


Table 3.5 Correlation between rainfall amounts and distribution during the incubation (23rd April to 27th July) and chick rearing periods (12th June to 5th October), 1958 to 1985.

	r	p
Total rainfall during chick period vs. total during incubation period.	0.2475	0.102
Number of days with more than twice daily average rainfall during chick period vs. same parameter for incubation period.	0.2964	0.063

Burrow Quality

The results described above indicate that breeding success over the Rhum shearwater colony as a whole is influenced by rainfall during the incubation period. Clearly, the effect of heavy rain is not the same for all breeding pairs, as there is no suggestion of a threshold in rainfall either side of which the colony experiences either very high breeding success or total failure. The linear relationship between hatching success and incidence of heavy rainfall suggests rather that there is a continuum in burrow quality with respect to likelihood of flooding. In order to investigate the significance of nest site choice in determining the probability of successful breeding, I attempted to quantify the likelihood of flooding for individual burrows. The derivation of this "flooding likelihood index" (hereafter abbreviated to F. L. I.) is described below:-

For a given discharge of water, the rate of infiltration into the soil below depends upon the soil permeability and the rate of runoff. Initially, I assume that the permeability of the soil is the same for all

burrows. Thus infiltration rate is primarily affected by the speed at which the water runs off the surface, with reduced infiltration at higher runoff velocities. For water flowing in channels the stream velocity is given by the Manning formula (Manning, 1889):-

$$\text{Stream velocity} = \frac{R^{2/3}S^{1/2}}{n}$$

where R is the hydraulic mean depth (area/wetted perimeter)
S is the bedslope
and n is the Manning roughness coefficient desribing the friction of the stream bed.

In considering the runoff of water on Hallival during rainfall, I assume R and n to be constants for all burrows so that:-

$$\text{Rate of runoff} \propto S^{1/2}$$

and $\therefore$ infiltration rate $\propto 1/S^{1/2}$

where S is the slope of the ground immediately above the nest chamber.

In addition to the rate at which water permeates the soil above a given nest chamber, the likelihood of that chamber actually flooding, will also depend on the depth of soil through which the water must pass so that:-

$$\text{Likelihood of flooding} \propto 1/D$$

where D is the depth of soil (in cm.) over the nest chamber. F. L. I. for burrows with chambers under soil is therefore defined as:-

$$\text{F. L. I.} = 1000/S^{1/2}D$$

For those burrows in which the nest chamber lies under a large rock, this index must be modified to take account of the impermeability of the rock. In these cases infiltration of water into the nest chamber will be reduced to water entering through the soil sides of the chamber from the surrounding area. In these instances F. L. I. is defined as:-

$$\text{F. L. I.} = 10/S^{1/2}$$

where S is the overall ground slope over 10m centered on the burrow in question.

The values of F.L.I. for rock-covered burrows fall within the lower part (better quality) of the range measured for those under soil. Thus the F.L.I. provides a non-linear measure of susceptibility to flooding.

Clearly the F.L.I. is a very crude index of susceptibility to flooding, as it takes no account of such features as the internal slope of the burrow, the presence of small stones in the substrate above the burrow chamber, or the effects on surface flow of very large rocks lying uphill of a burrow. However, any attempt to refine the index would have required the destruction of the burrows for which it was defined and would therefore have been self-defeating in attempting to relate breeding success to burrow quality. Also, the actual effects of such characteristics upon water flow and infiltration would be exceedingly difficult to assess.

Table 3.6 shows the results of a Chi^2 analysis of breeding outcome in relation to F. L. I. for 1984 and 1985 both seperately and combined.

Table 3.6 Chi^2 analysis of breeding outcome in relation to burrow quality.

a) 1984

	Flooding Likelihood Index ≤5.6 (Good burrows)	≥5.7 (Poor burrows)	Totals
Outcome			
No egg	O = 3 E = 5.8	O = 10 E = 7.2	13
Egg Failed to hatch	O = 16 E = 18.8	O = 26 E = 23.2	42
Egg Hatched	O = 15 E = 9.4	O = 6 E = 11.6	21
	34	42	76

$\chi^2 = 9.24$, d.f. = 2, $p < 0.01$

Table 3.6 cont.

b) 1985

Outcome	Flooding Likelihood Index ‹5.6 (Good burrows)	›5.7 (Poor burrows)	Totals
No Egg	O = 16	O = 22	38
	E = 21.4	E = 16.6	
Egg Failed to Hatch	O = 11	O = 6	17
	E = 9.6	E = 7.4	
Egg Hatched	O = 18	O = 7	25
	E = 14.1	E = 10.9	
	45	35	80

$\chi^2 = 6.06$, d.f. = 2, $p < 0.05$

c) 1984 and 1985

Outcome	Flooding Likelihood Index ‹5.6 (Good burrows)	›5.7 (Poor burrows)	Totals
No Egg	O = 19	O = 32	51
	E = 25.8	E = 25.2	
Egg Failed to Hatch	O = 27	O = 32	59
	E = 29.9	E = 29.1	
Egg Hatched	O = 33	O = 13	46
	E = 23.3	E = 22.7	
	79	77	156

It may be seen that eggs were both more likely to be laid, and more likely to hatch, in burrows less prone to flood in wet weather.

As shown in Table 3.7, a discriminant function analysis of breeding success in 1985, on the basis of physical characteristics of burrows, confirmed the importance of those characteristics which influence probability of flooding in influencing breeding success.

Table 3.7 Discriminant function analysis of breeding success in relation to characteristics of the burrow

The variables listed were available to separate burrows in the groups no egg laid, egg failed to hatch and egg hatched for 1985. Number of cases was 49.

Burrow Variable	Relative Ranking in Discriminant Function	Significance of Variable Alone in Separating Groups
(1) F. L. I.	1	$p<0.05$
(2) Proximity to other burrows	2	N.S.
(3) Altitude	3	$0.05<p<0.10$
(4) Slope over chamber	4	$p<0.05$
(5) Length	5	N.S.
(6) Tunnel curvature	Not Used	N.S
(7) Depth of soil over chamber		N.S.
(8) Slope over 10m centered on burrow		N.S.
(9) Presence/absence of rock over chamber		N.S.
(10)% of burrow length under rocks		N.S.
(11)No. of entrances		N.S.
(12)Area of main entrance		N.S.
(13)Main entrance aspect		N.S.

The overall significance (p) of the function derived was 0.007 and it correctly classified 69.4% of cases.

Relationship between Bird Quality and Burrow Quality.

The direct influence of burrow quality in determining the probability of successful breeding was confirmed by my observations of eggs being washed out of flooded burrows in 1985. However, there may also be an indirect effect involved. If, as might be expected, individuals vary in their ability to breed successfully, and if less proficient birds occupy poorer quality burrows, then the reduced probability of successfully hatching an egg in these burrows could, in part, arise from their occupation by "poor quality" birds. In terms of a bird's ability to hatch

an egg successfully, a critical factor is likely to be the ease with which the bird can find sufficient food to maintain its body weight during incubation. Therefore, in order to examine any correlation between burrow quality and bird quality, it is necessary to find some criterion which reflects foraging ability and which can be measured in the field.

The most straightforward index of foraging ability might be a measure of body reserves as indicated by weight adjusted to allow for inherent differences in body size. Slagsvold's (1982) condition measure for hooded crows ie. weight per unit tarsus length is one such index. However, in a species such as the Manx shearwater which undergoes large fluctuations in weight over short periods eg from beginning to end of an incubation shift, it would only be valid to compare individuals if they were all at exactly the same stage of the breeding cycle (cf. Chp. 2). This is not possible in practice and so some secondary indicator of condition is required.

In order to discover if any such simple indicator of relative condition existed, I examined the biometrics of the adults weighed during three nights in July 1986. Most birds measured were probably non-breeders, as these birds spend much more time sitting outside burrows than breeding birds and are therefore much easier to find and catch, but a few were clearly carrying food for chicks. In order to eliminate these birds from the sample the heaviest 10% of birds on each night were excluded from the analysis.

In the first stage of the analysis, I examined simple correlations between weight and body dimensions to determine which of these dimensions best indicate the actual structural size of the bird. The results are given in Table 3.8. Of the four body dimensions considered, head length was most consistently correlated with weight, and so this dimension was used in further analysis.

Table 3.8 Weights of adults found sitting on the surface on Hallival in July 1986 in relation to body dimensions

	22-23/7/86 (n = 93)	28-29/7/86 (n = 102)	29-30/7/86 (n = 91)
Weight vs. wing	r = 0.3688	r = 0.1827	r = 0.2873
	p < 0.001	N.S.	p < 0.01
Weight vs. bill	r = 0.1170	r = 0.1549	r = 0.1853
	N.S.	N.S.	N.S.
Weight vs. head	r = 0.2299	r = 0.4151	r = 0.4205
	p < 0.05	p < 0.001	p < 0.001
Weight vs. tarsus	r = 0.2971	r = 0.1847	r = 0.4264
	p < 0.01	N.S.	p < 0.001

The second part of the analysis was aimed at discovering whether condition, as indicated by weight per unit head length, was itself correlated with any of the body dimensions measured. The results of this analysis are given in Table 3.9. The results of this suggested that whereas condition is positively correlated with wing length it tends to be negatively correlated with bill length. The relationships between weight and body dimensions described above, are confirmed by a multiple regression analysis of the dependency of weight upon wing, bill, head and tarsus lengths for all three nights' data pooled together. The regression equation derived was:-

weight = 6.2415(head) + 1.034(wing) - 4.186(bill) - 226.555

This regression accounted for 18% of the variation in weight with head length alone explaining 12.3%. On the basis of these analyses I used wing length as an index of bird quality in assessing the possibility of a relationship between bird quality and burrow quality.

As male shearwaters are apparently primarily responsible for selecting and defending burrows (James, 1985), I restricted analysis of bird quality in relation to burrow quality to males only. Fig. 3.2 shows the regression of male wing length on F. L. I. for observation burrows in

Fig. 3·2 MALE WING LENGTH IN RELATION TO BURROW QUALITY

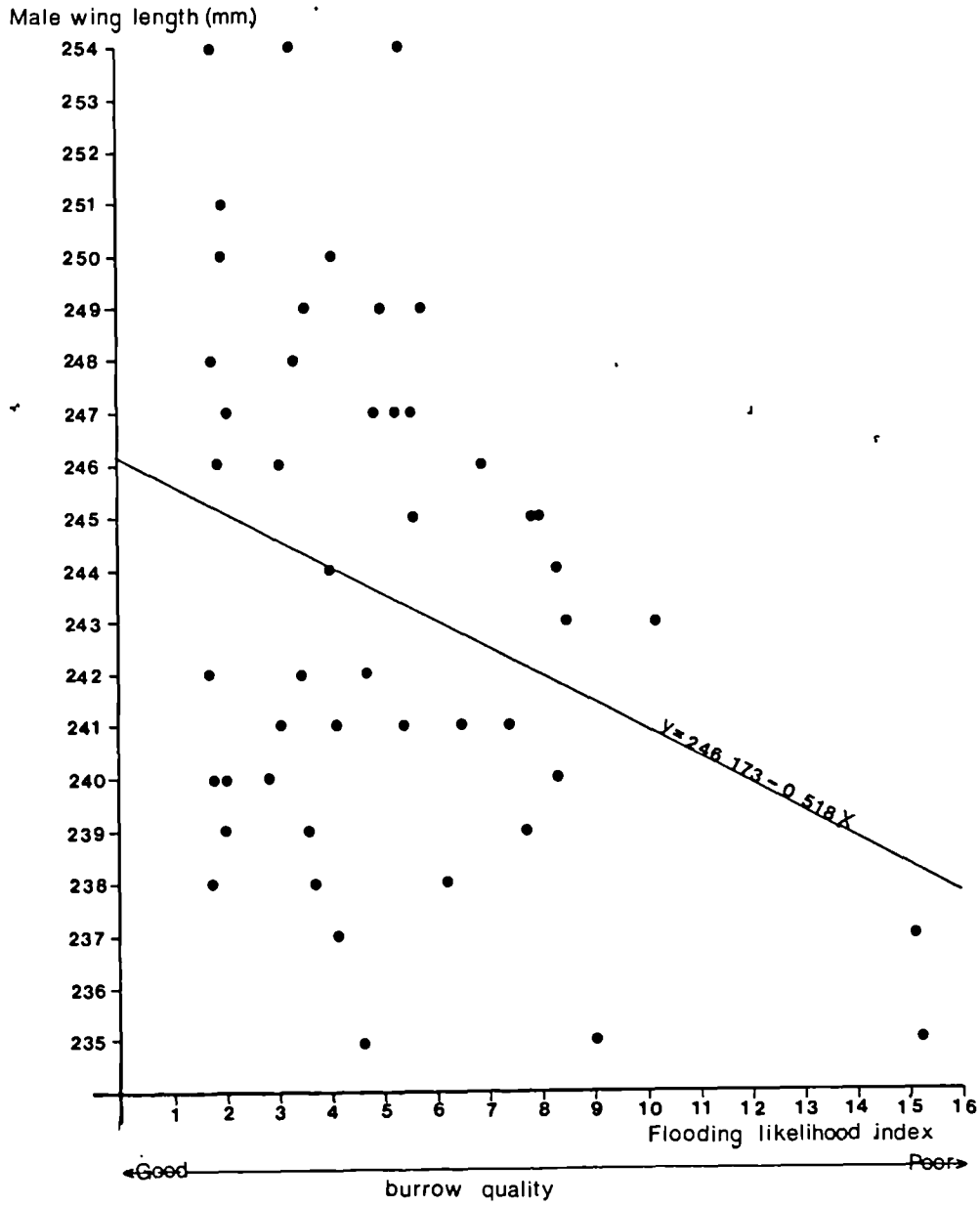


Table 3.9 Condition (weight/head length) of adults found sitting on the surface on Hallival in July 1986 in relation to body dimensions

	22-23/7/86 (n = 93)	28-29/7/86 (n = 102)	29-30/7/86 (n = 91)
Condition vs. wing	r = 0.2924 p < 0.01	r = -0.0570 N.S.	r = 0.1648 N.S.
Condition vs. bill	r = -0.1977 N.S.	r = -0.0969 N.S.	r = -0.2647 p < 0.02
Condition vs. head	r = -0.1649 N.S.	r = 0.0391 N.S.	r = 0.0050 N.S.
Condition vs. tarsus	r = 0.1169 N.S.	r = 0.0105 N.S.	r = 0.2233 p < 0.05

1985, the year for which most data were available. The regression coefficient, r, is -0.3166 and the relationship is significant at the 5% level. This does suggest that better quality burrows tend to be occupied by those males most capable of maintaining high body reserves. This may arise from increased ability to spend more time in the colony during the pre-laying period defending burrows, but I have no direct information on this. An alternative explanation for the observed correlation between wing length and burrow quality could be that wing length is simply a measure of size, and that larger birds are able to obtain and defend better quality burrows. However, two pieces of evidence tend to refute this. Firstly, wing length is not consistently correlated with head and bill length (22-23/7/86:- n = 93, r = 0.1978, N.S.; 28-29/7/86:- n = 102, r = 0.2748, p < 0.01), which suggests that it is not a straightforward indicator of body size. Secondly, unlike wing length, head and bill length was not significantly correlated with flooding likelihood index in 1985 (n = 50, r = 0.0034, N.S.), which suggests that body size as such does not determine ability to occupy better quality burrows.

Gaston and Nettleship (1981), in their study of Brunnich's guillemots nesting in arctic Canada, used timing of breeding as an indicator of female quality and found some

significant and consistent trends between hatching date and certain nest site characteristics. However, I found no significant correlation between laying date and F.L.I. in either 1984 or 1985 (1984, n = 70, r = 0.0945, N.S.; 1985, n = 36, r = 0.1482, N.S.).

Burrow Selection

As choice of burrow is apparently of importance in determining the probability of successful breeding, it might be expected that Manx shearwaters on Rhum should elect to occupy high quality burrows. Table 3.10 shows a Chi^2 analysis of the degree of faithfulness of breeding birds to their 1984 burrow in 1985, in relation to their breeding success in 1984. These results indicate that males are more likely to abandon their burrows following a breeding failure than a breeding success in the previous year. Unfortunately, insufficient data were available to assess what proportion of those birds which failed to return to the same burrow actually attempted to breed in a different burrow, and what proportion did not breed at all. By contrast female movement appears unrelated to previous season's breeding outcome.

Table 3.10 Movement of breeding adults from their burrows in relation to breeding success

(a) Males

1984 \ 1985	Occupying same burrow	Alive but not in same burrow	Total
Egg Failed to Hatch	O = 18 E = 23.0	O = 31 E = 26.0	49
Egg Hatched	O = 12 E = 7.0	O = 3 E = 8.0	15
	30	34	64

$\chi^2 = 8.75$, d.f. = 1, $p < 0.01$

Table 3.10 cont.

(b) Females

1984 \ 1985	Occupying same burrow	Alive but not in same burrow	Total
Egg Failed to Hatch	O = 18 E = 20.0	O = 27 E = 25.0	45
Egg Hatched	O = 10 E = 8.0	O = 8 E = 10.0	18
	28	35	63

$\chi^2 = 1.26$, d.f. = 1, N.S.

Note:-

The observed totals of birds alive but not in the same burrows are given by:-

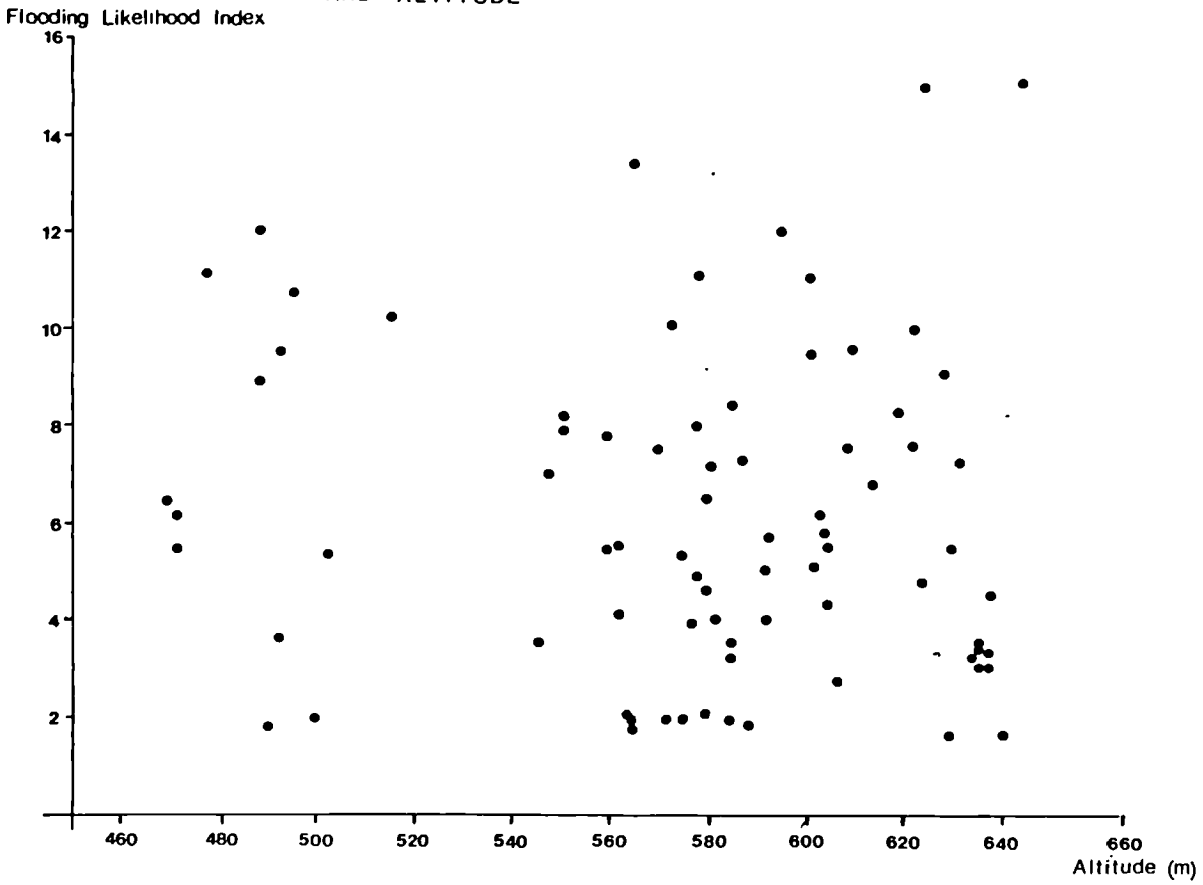
(0·9x birds found alive in 1984) − birds in same burrows in 1985

This assumes an average annual adult survival rate of 0.90 (Brooke, 1977).

Insufficient data were available to determine the incidence of divorce in relation to breeding outcome. Brooke (1978a) found that the incidence both of movement of unchanged pairs between burrows and of divorce were greater following breeding failure than following breeding success.

Of 10 known males which moved to different burrows from 1984 to 1985, 5 moved to better quality burrows (ie. lower F. L. I.), and 5 to poorer quality ones. There is therefore no obvious tendency for movement to better quality burrows. Indeed, it seems likely that there may in fact be no means by which birds can assess burrow quality other than by attempting to breed. Although hill slope does increase with altitude in the study area (regression of S on altitude:- $r = 0.4436$, $p < 0.001$), local variations in topography and the random scatter of boulders over the hillside mean that there is no correlation between F. L. I. and altitude as is illustrated in Fig. 3.3. The month of April, which encompasses the main part of the prelaying

Fig 33 RELATIONSHIP BETWEEN BURROW QUALITY AND ALTITUDE



period, is on average the second driest in the year on Rhum (N.C.C., 1974), so that burrows are unlikely to flood at this time and thus give any direct indication of flooding likelihood later in the breeding season.

Discussion

In their discussion of habitat selection by Atlantic Alcidae, Birkhead and Harris (1985) divide the process into three main levels, namely colony location; choice of habitats within a colony; and the choice of breeding site within a given habitat. In choosing to nest on Rhum and its neighbouring islands, Manx shearwaters are able to exploit the rich marine resources of the Hebridean area which support ca one million breeding pairs of 22 species of seabirds (Bourne and Harris, 1979). In addition to its proximity to rich feeding grounds, Rhum also meets the three criteria identified by Storey (1986) as being of value in identifying potentially suitable breeding sites for this species, namely a low population density of predatory gulls (total of 53 pairs of great black-backed gulls nesting on Rhum in 1984, D. Hale, pers. comm.); the presence of rock-earth habitat suitable for excavation of long burrows; and weather conditions resulting in many nights of low illumination so that prospecting birds can visit the colony in relative safety from avian predators.

On Rhum, the location of the colony at high altitude may reflect both predation pressure (Chapter 6), and the free-draining nature of the sandy soil of the south-east ultrabasic ridge, which contrasts markedly with the often waterlogged peat which blankets most other parts of the island. The restriction in distribution of various shearwater species nesting in wet climates to steep slopes has been mentioned by several authors including Harrow (1965) for Hutton's shearwater on South Island, New Zealand; Kepler et al. (1979) for Newell's shearwater in Hawaii; and Byrd et

al. (1983) for wedge-tailed shearwaters also in Hawaii. Similarly, Grant and Nettleship (1971) noted that puffins breeding in cliff gullies in Iceland avoided those with low slopes subject to flooding and solifluction.

Within the main colony area, burrow densities are greatest in the boulder strewn "greens", the rich vegetation of which has developed as a direct result of the shearwaters' presence (Wormell, 1976). Less stable habitats such as boulder fields, scree slopes and eroding earth banks are apparently less favoured. Grant and Nettleship (1971) found that total boulder perimeter within study plots influenced puffin breeding density in Iceland, and suggested that individual boulders provide useful landmarks to enable birds to land close to their burrows and hence minimise risk of predation. It seems likely that the distinctively shaped boulders scattered over the "greens" in the Rhum shearwater colony may also be important in this respect (cf. Appendix 1).

The results presented in this chapter indicate that on Rhum Manx shearwaters' nesting burrows vary in quality according to their probability of flooding, and that there is therefore selective pressure for birds to nest in the higher quality burrows. The impact of rainfall on burrow-nesting species is seldom referred to except in instances where exceptional storms actually destroy burrows for example of wedge-tailed shearwaters in Hawaii (Whittow, 1979; Byrd et al.,1983). Similarly Boersma et al. (1980) refer to there being some mortality of fork-tailed storm petrel chicks in Alaska in wet burrows after bad weather, while Serventy and Curry (1984) noted occasional egg loss due to flooding of short-tailed shearwater burrows situated on low ground after exceptionally heavy summer rainstorms. Hornung and Harris (1976) compared sub-colonies of the puffin population on the Farne Islands with respect to the timing of drying out of burrows during the wet spring of 1975. They concluded that the observed pattern of laying dates, namely synchrony within

sub-colonies but a considerable range over the colony as a whole, was controlled by the time at which burrows dried out in spring. In this instance, it was clearly adaptive for those birds in the wetter parts of the colony to delay laying until their burrows were dry rather than to waste energy by laying in wet nest sites. Ashcroft (1976, in Birkhead and Harris 1985) found no correlation between breeding success and burrow position, ground slope, burrow density, burrow length or burrow depth among puffins nesting on Skomer which implies that burrow flooding at that site did not occur during the course of the study.

The effect of heavy rain on the Manx shearwaters on Rhum is apparently greatest during the incubation period. The annual pattern of rainfall on the island is such that flooding in the colony is unlikely during the pre-laying period, so that the birds are unable to predict the probability of flooding occurring. Rather, they are apparently able to assess the quality of a particular burrow only by attempting to breed in it. This is at variance with the situation described by Potts et al. (1980) for shags nesting on the Farne Islands. There, it was possible to rank nest site quality in terms of variables relating to exposure to the elements, nest capacity and ease of access to the sea. The number of young fledged per pair was highly significantly correlated with nest site quality independently of the pairs' breeding experience, although younger birds, which return to the colony later than experienced breeders, were generally excluded from the best sites. Following a natural removal experiment in which large numbers of breeding adults died during a "red tide", most of the survivng males moved to different nest sites, and 80% of them either maintained or improved their nest site quality. Potts et al. concluded that male shags are able to recognise good quality nest sites without direct experience of conditions at a given site.

The adaptive significance of birds changing territory or nest site in response to breeding failure has

been discussed by several authors. In her study of black skimmer colonies nesting on low lying salt marshes in New Jersey, Burger (1982) confirmed that colonies were indeed more likely to be re-occupied if overall breeding success at that site had been high in the previous season. She also discovered that the incidence of colony movement following breeding failure was related to the extent to which failure in one year was indicative of a high probability of future failures at the same site. Thus colonies where breeding failure was the result of predation by other species nesting on the same site were more likely to be abandoned than those where breeding failure had resulted from tidal flooding which was not predictable from year to year at any given site. Similarly, Blancher and Robertson (1985) found that the breeding distribution of eastern kingbirds around shallow lakes in Ontario, was related to the consistent, and therefore predictable, differences in breeding performance in different territories. In particular the kingbirds preferred those territories in which egg laying dates were generally earliest while their distribution was less affected by predation rate. This was particularly interesting, as while predation rate had a greater impact on breeding successs than did laying date, it was less predictable between years within individual territories.

On Rhum Manx shearwaters are not subject to predation of eggs or young from burrows (Chapter 6), so that predation does not directly influence breeding outcome and hence is not a determinant of burrow quality. The siting of the colony on steep slopes may however serve to reduce avian predation of adults. Nettleship (1972) concluded that the greater breeding success of puffins on slope habitats on Great Island, Newfoundland over those on level ground, was attributable to the greater impact of disturbance by gulls at level sites. Puffins at these sites were slower to become airborne and as a result were more prone to mass panic flights at the approach of gulls.

However, the main selection pressure on Manx shearwaters on Rhum to occupy certain burrows in preference to others, appears to result from the variation in burrow quality with respect to flooding. Although annual variations in rainfall amounts and distribution will result in varying percentages of the burrows flooding in each season, the likelihood of flooding in the poorest burrows is consistently high. It is therefore advantageous for birds to occupy the better quality burrows.

As I have no information on the ages of the birds in my study area, I am unable to examine the relationship between breeding experience and burrow quality. However, given the fact that prospecting birds visiting the colony over several years prior to breeding spend little time on land until after the breeding season has commenced (Brooke 1977), it is unlikely that many of these young birds will initially find and retain ownership of the best quality burrows. First time breeders will probably tend to nest in burrows which were not occupied in the previous season, having been rejected by experienced breeders. Thus the tendency of birds to move following breeding failure and of older birds to return earlier to the colony will probably result in more experienced birds occupying better burrows. This would be analagous to the situation in the Farne Islands shag population (Potts et al., 1980), and would further tend to reduce breeding success at the poorest quality nest sites as breeding experience has been found to be an important determinant of breeding success in many species of seabird eg. kittiwake (Thomas, 1983), fulmar (Ollason and Dunnet, 1978), Manx shearwater (Brooke, 1978a).

In addition to any uneven distribution of birds of different ages with respect to burrow quality, there is some suggestion that competition among experienced breeders results in poorer quality birds occupying poorer quality burrows. On Great Island, Newfoundland, Nettleship (1972) found the mean body weight of male puffins to be greater at

the higher quality slope habitat than on the level ground. Mean wing lengths of the two groups were the same so that there appeared to be a genuine difference in condition between males from the different habitats.

On the Farne Islands, Potts et al. (1980) found an inverse correlation between the number of shag nest sites occupied in any one year and the mean quality of those sites. The same is probably true of the Rhum shearwater colony where the better quality nest sites may be reused by the same pairs over many seasons. In this situation any increase in colony size would result in a reduced annual reproductive output per pair. As most male Manx shearwaters return to their natal colony to breed (Brooke, 1978b) there would follow a reduction in recruitment relative to adult mortality until the equilibrium point of equal annual mortality and recruitment were reached. At this point the colony could only continue to expand if there was a net immigration of recruits of both sexes into the colony. This has apparently occured in the Farne Islands shag colony which may be regarded as one part of a larger population. In the Manx shearwater there is to date no evidence of significant net movements between colonies (Harris 1972, Brooke 1978b, N. McKee pers. comm.).

In conclusion, it would appear that the availability of good quality nest sites may ultimately limit the size of the shearwater population on Rhum. Since burrow quality in this instance is primarily defined as the likelihood of flooding, any major alteration of the island's rainfall regime would result in a change in the maximum potential colony size. This is discussed further in Chp. 7.

Chapter 4

TIMING OF BREEDING, EGG DIMENSIONS, AND FLEDGING WEIGHTS

Introduction

In environments where there are marked seasonal variations of climate, and hence in primary productivity, it is selectively advantageous for organisms to breed at the time of year when the probability of successfully producing independent young is greatest. Amongst birds nesting in the temperate and polar regions, a common ultimate factor determining timing of reproduction is the temperature-related cycle of food abundance. In these regions it is advantageous for nidicolous birds to time their breeding such that young are reared at the time of peak availability of appropriate food, thus maximising potential provisioning rates (Lack, 1966). However the seasonality in climate may also place constraints on prospective breeders. For example, food supplies early in the season may be insufficient to allow females to build up sufficient reserves for egg formation (Perrins, 1970) or nest sites may be inaccessible due to snow or ice (Sealy, 1975). Individuals vary in their ability to exploit available resources, and in many species this leads to a range in timing of breeding within colonies and years.

Long-term studies of Manx shearwaters on Skokholm have demonstrated that survival of young from fledging to return to the colony when two or more years old is related to timing of fledging. There is generally a negative correlation between survival and fledging date although the

strength of this effect varies between years (Perrins, 1966; Brooke, 1977). In addition, there is a strong positive relationship between fledging weight and subsequent survival, and fledging weight shows a seasonal decline (Perrins et al., 1973). Brooke's (1977) egg-swapping experiments suggested that this decline in fledging weight over time is probably due to deterioration in food availability over the chick rearing period, rather than to any tendency for adults more proficient at provisioning chicks to breed earlier.

In this chapter I present data on fledgling weights and timing of breeding on Rhum. I also examine the significance of fledging weight in determining the probability of survival. In, addition I investigate the constraints leading to the observed variations in timing of breeding and discuss the shearwaters' response to these constraints.

Methods.

Most of the data presented here were derived from the observation burrows described in Chapter 1. Laying, hatching and fledging dates were established through regular checking, at daily intervals where possible, of these burrows at the appropriate stages of the breeding cycle. Additional data on fledging weights in relation to date were obtained from chicks found sitting on the surface of the colony outside their burrows at night just prior to fledging. This behaviour apparently enables fledglings to exercise their wings on the ground for a few nights before actually departing from the colony (Perrins et al., 1973).

The egg volume index used to describe the relative sizes of individual eggs was calculated as (length in cm.) x (maximum breadth in cm)^2 (Brooke, 1978a) where these dimensions were measured to the nearest mm. In 1985 and 1986 newly laid eggs were also weighed to the nearest g.

Female condition index was calculated as weight ÷ tarsus following Slagsvold's (1982) method for hooded crow.

This is a simple means of correcting for body size when comparing weights.

Flight patterns of shearwaters at sea were observed on 6 occasions from the ferry crossing between Rhum and the mainland. Complete periods of flapping and gliding flight were measured using a stopwatch.

Results.

Relationship between fledging weight and date.

In both 1984 and 1985 the weights at fledging of chicks in my observation burrows showed a tendency to decline with later hatching date (Fig. 4.1). However this relationship was only significant ($p = 0.04$) when the data from both years were pooled, due to the small sample sizes in each year. As mean fledging weight did not differ between these years (1984:- mean = 468.7g, S.E. = 14.67; 1985:- mean = 471.6g, S.E. = 12.60; $p > 0.05$), and mean hatching date was also similar in both years (1984:- mean = 8.21, S.E. = 1.302; 1985:- mean = 10.65, S.E. = 0.868; $p > 0.05$ where 1 = 23rd June) this probably indicates a genuine seasonal decline in fledging weight. This is further supported by the data presented in Fig. 4.2 which illustrates the decline in weight with date of ringing of those fledglings picked up on the hillside. The relationship in 1984 was not quite significant ($p = 0.06$), those in 1985 and 1986 were highly so ($p < 0.001$).

Among the chicks which fledged from my observation burrows in 1984 there was a highly significant decline in fledging weight with age at fledging ($n = 14$, $r = -0.791$, $p < 0.001$). In 1985 there was no significant relationship between these two variables. In both years there was a tendency for later hatching chicks to fledge older but this relationship was not significant ($p = 0.11$ in both years). When the data from both years are pooled* the correlation between fledging age and hatch date is significant ($n = 27$, $r = -0.432$, $p < 0.05$). In both years there was a highly

* excluding randomly data from one year in cases where the same burrow produced fledglings in both years.

Fig.4·1 FLEDGING WEIGHT IN RELATION TO HATCHING DATE.

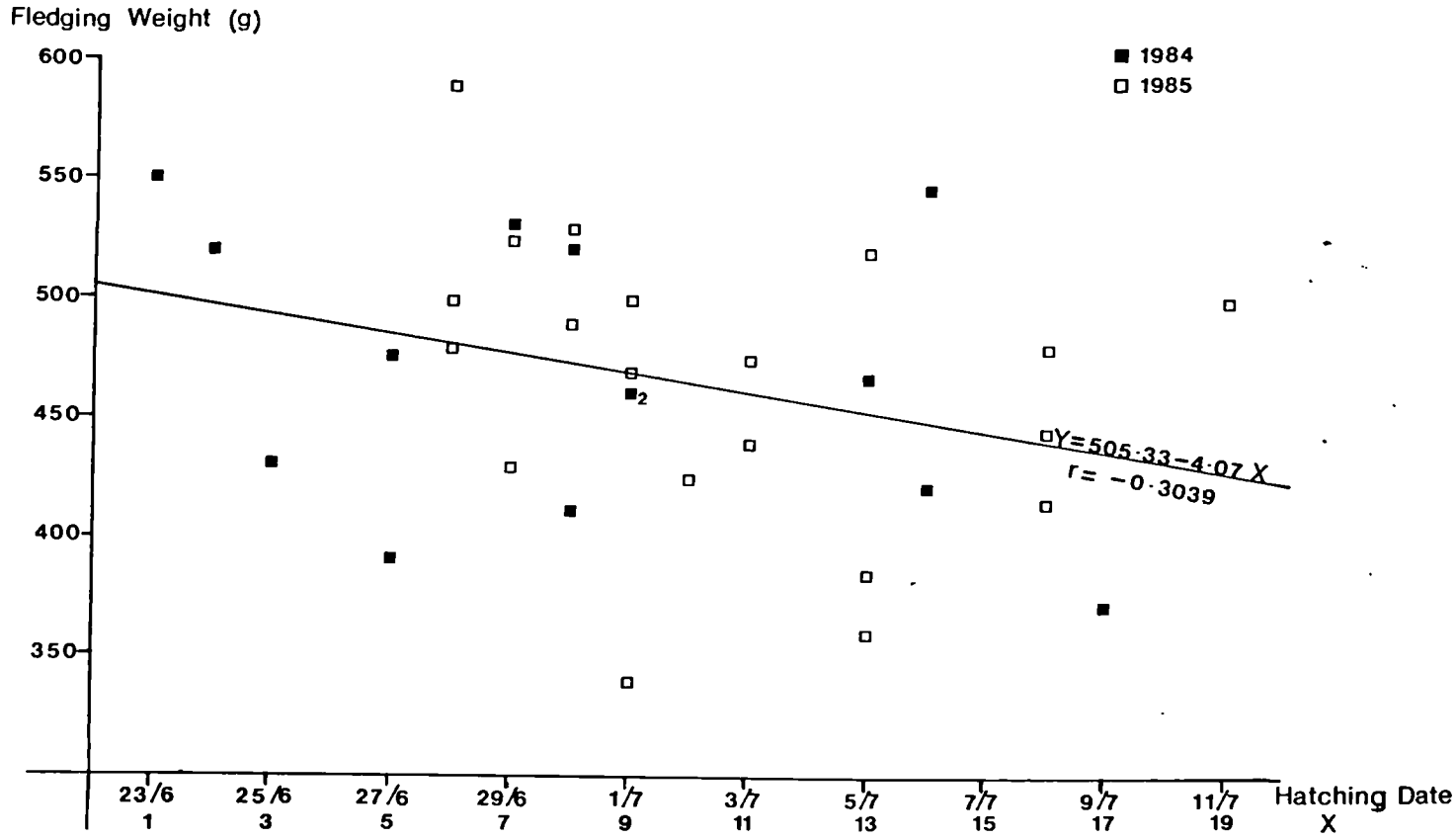
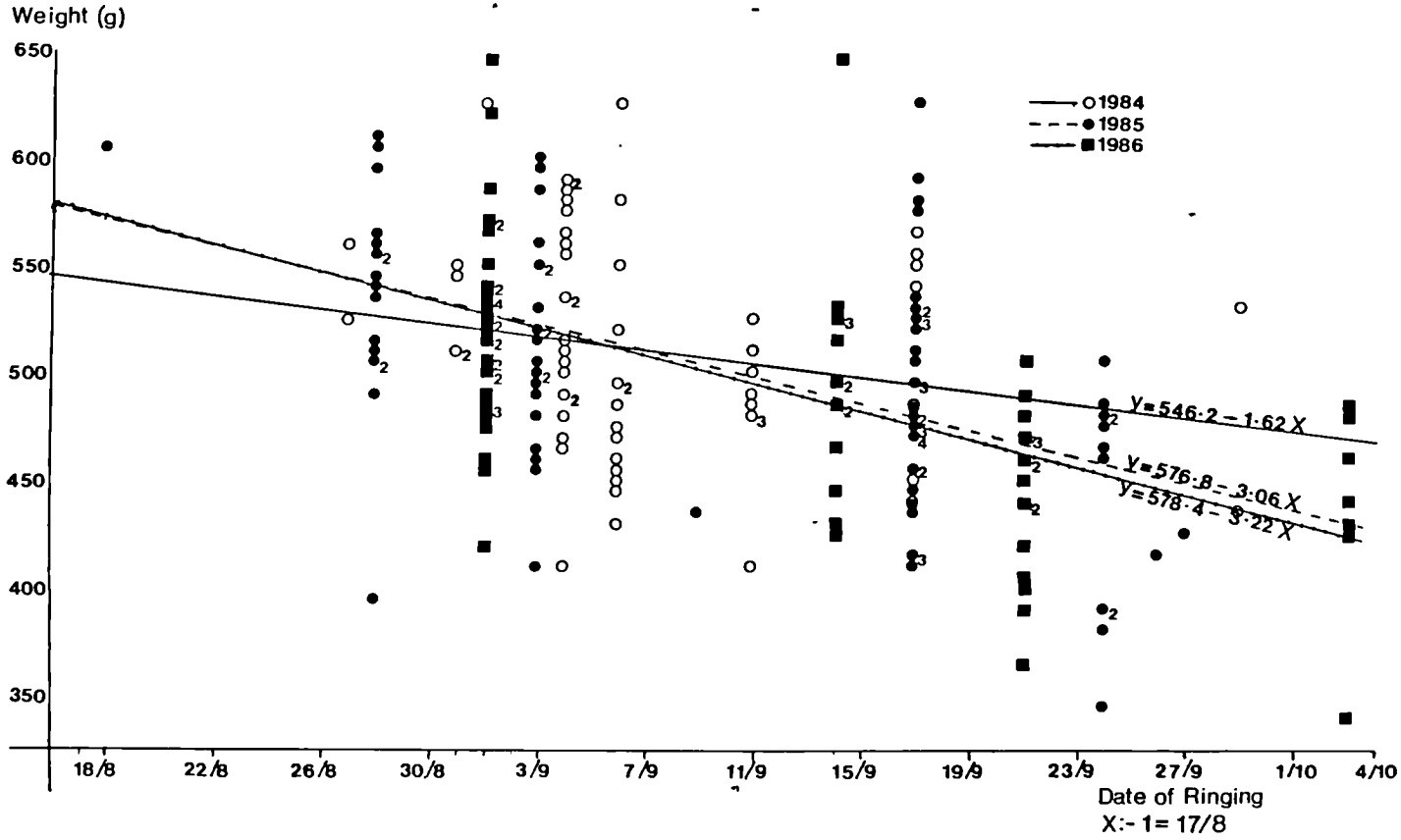


Fig. 4·2 SEASONAL DECLINE IN WEIGHTS OF FLEDGLINGS



significant positive correlation between age and date of fledging as illustrated in Fig. 4.3 (1984, r = 0.724, p <0.001; 1985, r = 0.757, p <0.001). As found by Brooke (1977) on Skokholm, in neither year was there any correlation between peak weight and hatching date. This suggests that the seasonal decline in fledging weight arises from increasing difficulty for parents in provisioning chicks between peak weight and fledging. The observed tendency for later hatched chicks to delay fledging supports this.

Timing of laying

Laying dates of eggs in my observation burrows in 1984, 1985 and 1986 are shown in Fig. 4.4. The bars indicate the actual numbers of eggs laid in each three day period. The lines show the cumulative percentage of eggs laid by the end of each three day period in each year. The arrows indicate the median laying date in each year. The median laying date in 1986 was significantly later than either 1984 or 1985 (Mann-Whitney U tests, $p < 0.001$). In several species of auks there is evidence that late seasons are associated with lower than average sea surface temperatures eg. rhinoceros auklet (Vermeer, 1980); all species of Atlantic auks (Birkhead and Harris, 1985). Hedgren (1979) found that fledging dates of common guillemots breeding in the Baltic were negatively correlated with February to May air temperatures in that area. Similarly, Perrins (1973) reported a negative correlation between median laying dates of great tits and spring air temperatures, and attributed this to reduced food abundance for egg formation in cooler years. Average mean daily air temperatures (ie. the mean of the maximum and minimum temperatures recorded each day) between 1st February and 31st May recorded at Kinloch meteorological station were 7.05° (S.E. 0.820) in 1984, 6.69° (S.E. 0.933) in 1985 and 5.57° (S.E. 1.052) in 1986. The difference between 1984 and 1985 was not significant ($t = 0.894$, $p > 0.30$) while 1986 was significantly cooler than

Fig. 4·3 FLEDGING AGE IN RELATION TO FLEDGING DATE

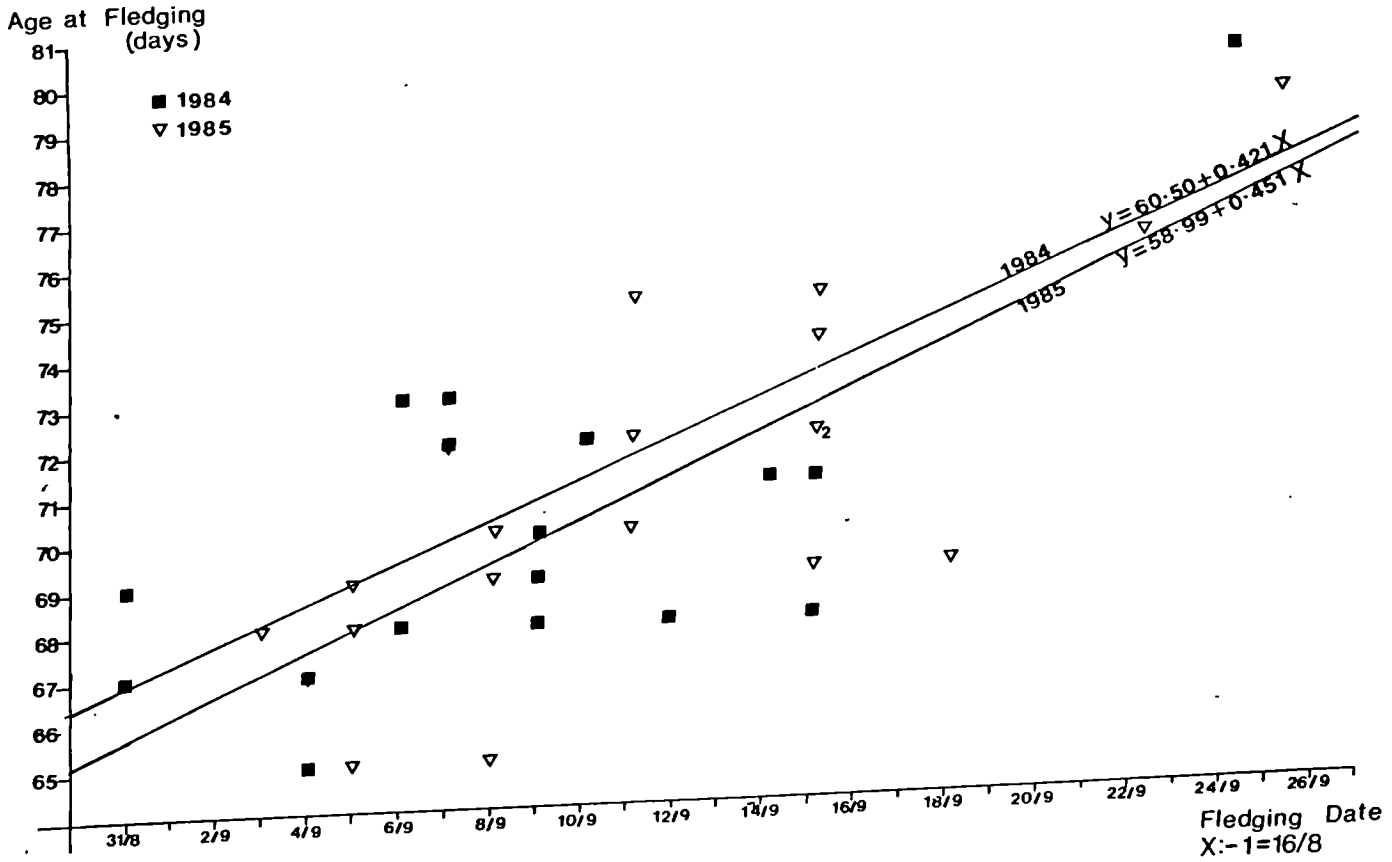
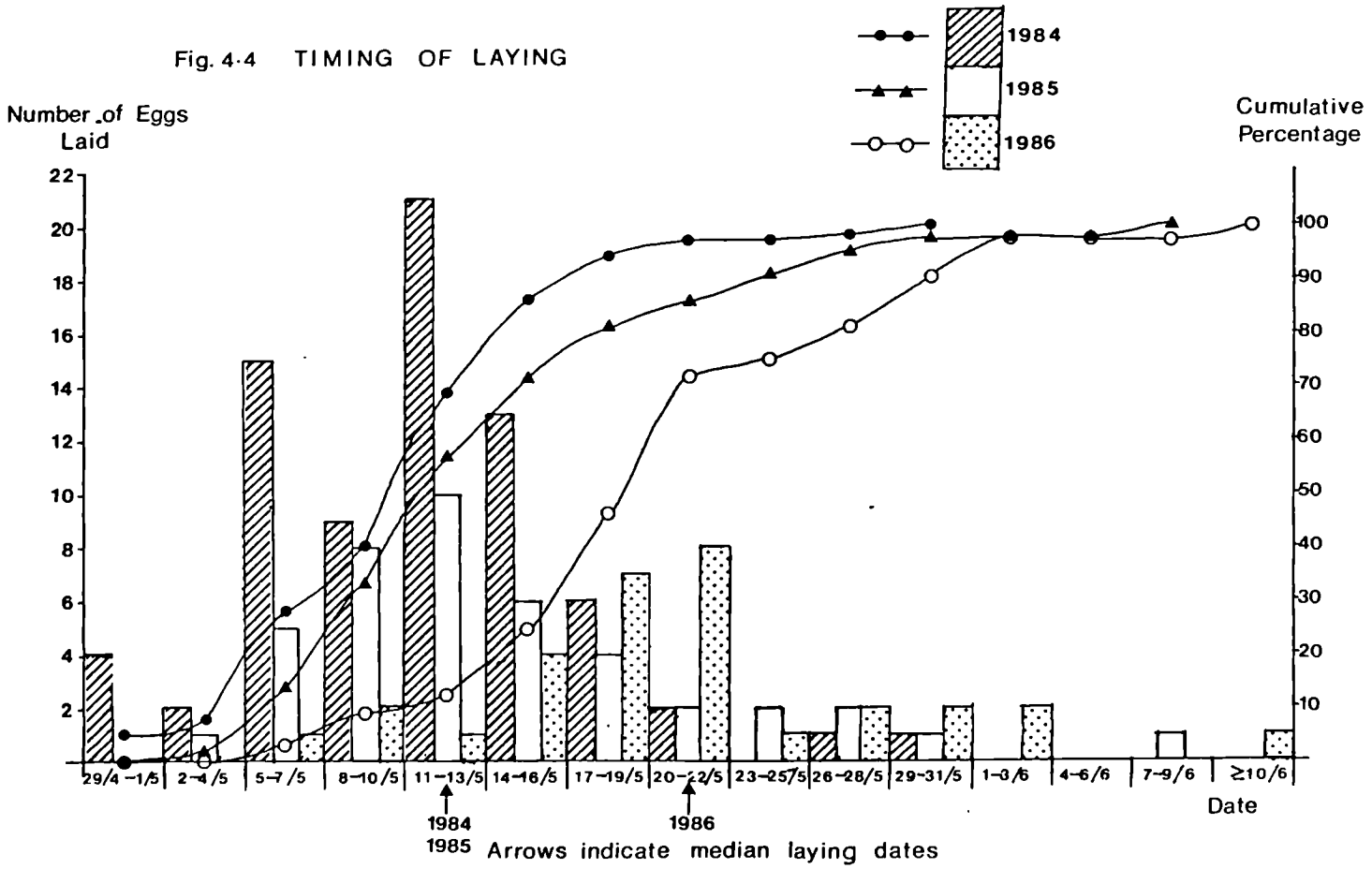


Fig. 4·4 TIMING OF LAYING



either 1985 (t = 2.610, p < 0.01) or 1984 (t = 3.546, p < 0.001). Mean sea surface temperatures at 56-57° North, 5-7° West in March to June of 1984 to 1986 are shown in Table 4.1. Wind strengths recorded at Benbecula, ca. 80km N.W. of Rhum, from March to May in 1984 to 1986 are shown in Table 4.2. These data indicate that sea surface temperatures from March to early May 1986 were half a degree lower than in the preceeding two years but that by June they had almost recovered to the seasonal norm. The occurrence of winds exceeding force 5 (ie. greater than 21 knots) in March was low in 1984 and high in 1986. The frequency of strong winds during April was similar in all three years, but winds of force 6 or over were significantly more frequent in May 1986 than in the same month in the previous two years.

Table 4.1 Mean monthly sea surface temperatures, °C, at 56-57°N, 5-7°W, March to June 1984-1986.

	1984	1985	1986
March	7.1	7.1	6.6
April	7.3	7.3	6.8
May	8.5	8.5	8.1
June	10.7	10.7	10.6

Table 4.2a Numbers of hours in which winds blew above or below 21 knots at Benbecula in March, 1984 to 1986.

	1984	1985	1986	Totals
Wind < force 6	671	583	495	1749
Wind > force 6	73	161	245	479
Totals	744	744	740	2228

Table 4.2b Numbers of hours in which winds blew above or below 21 knots at Benbecula in April, 1984 to 1986.

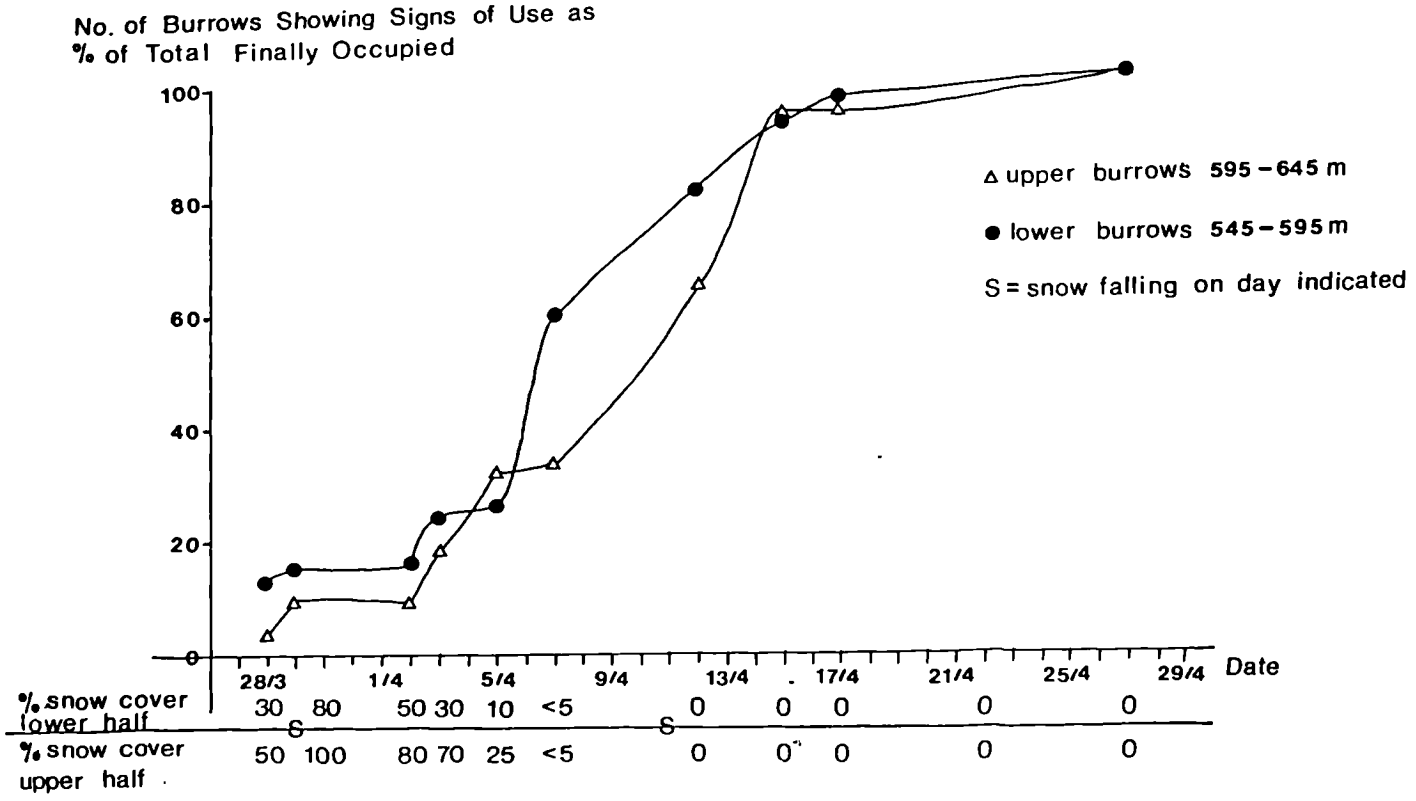
	1984	1985	1986	Totals
Wind < force 6	650	642	649	1941
Wind ≥ force 6	70	78	71	219
Totals	720	720	720	2160

Table 4.2c Numbers of hours in which winds blew above or below 21 knots at Benbecula in May, 1984 to 1986.

	1984	1985	1986	Totals
Wind < force 6	727	723	652	2102
Wind ≥ force 6	17	21	92	130
Totals	744	744	744	2232

In 1984 I recorded dates by which most of the observation burrows first showed signs of occupation such as fresh digging or droppings at the entrances. Fig. 4.5 illustrates the rise in numbers of burrows thus judged to be in use during the prelaying period. The data are from burrows lying within 5m either side of a fixed transect line running straight up a slope between 545m and 645m altitude. Snow showers were frequent during this period so that the slope was at least partially snow covered for much of the time. During periods of thaw between snowfalls there was a very obvious difference in rates of melt between the lower and upper halves of the transect. This resulted in a higher average percentage snow cover along the top half of the transect as is indicated by the figures below the abscissa.

Fig. 4·5 OCCUPANCY OF OBSERVATION BURROWS IN 1984



Comparison of the patterns of burrow occupancy along the lower and upper halves of the transect illustrate earlier and more rapidly increasing use of the lower, more easily accessible, burrows. Fig. 4.6 illustrates the positive correlation between laying date and first occupancy of these burrows in 1984 ($r = 0.371$, $p < 0.01$). Brooke (1977) also found Manx shearwater laying date to be correlated with the date on which the male first reoccupied the burrow. These results suggest that those birds nesting in parts of the colony experiencing prolonged snow cover in the early spring may tend to lay later than birds with burrows less frequently snow-covered. This is confirmed by comparison of the median laying dates in burrows along the lower (n = 31, median = 8-10th May) and upper (n = 31, median = 11-13th May) halves of the transect (Mann Whitney U test, $p < 0.01$). Sealy (1975) found that follicular development in least auklets was more rapid in females from areas of the colony with earlier snow melt. Females from sites with prolonged snow cover showed delayed follicular maturation but were unable to delay laying indefinitely. This resulted in some eggs being laid on surface snow if snow melt was prolonged. Similarly, Harrow (1976) found that egg laying among Hutton's shearwaters in mountains in South Island, New Zealand was delayed in years of heavy snow cover.

Data on the relationship between laying dates and female dimensions in 1984 and 1985 are summarised in Table 4.3. There is little indication of any strong correlation between female size and date of laying, although in 1985 females with longer bills tended to lay earlier than smaller birds. These results concur with Brooke's (1978a) data which revealed no general significant correlation between laying date and female body size.

Fig. 4·6 LAYING DATE IN RELATION TO DATE BY WHICH BURROW FIRST OCCUPIED 1984

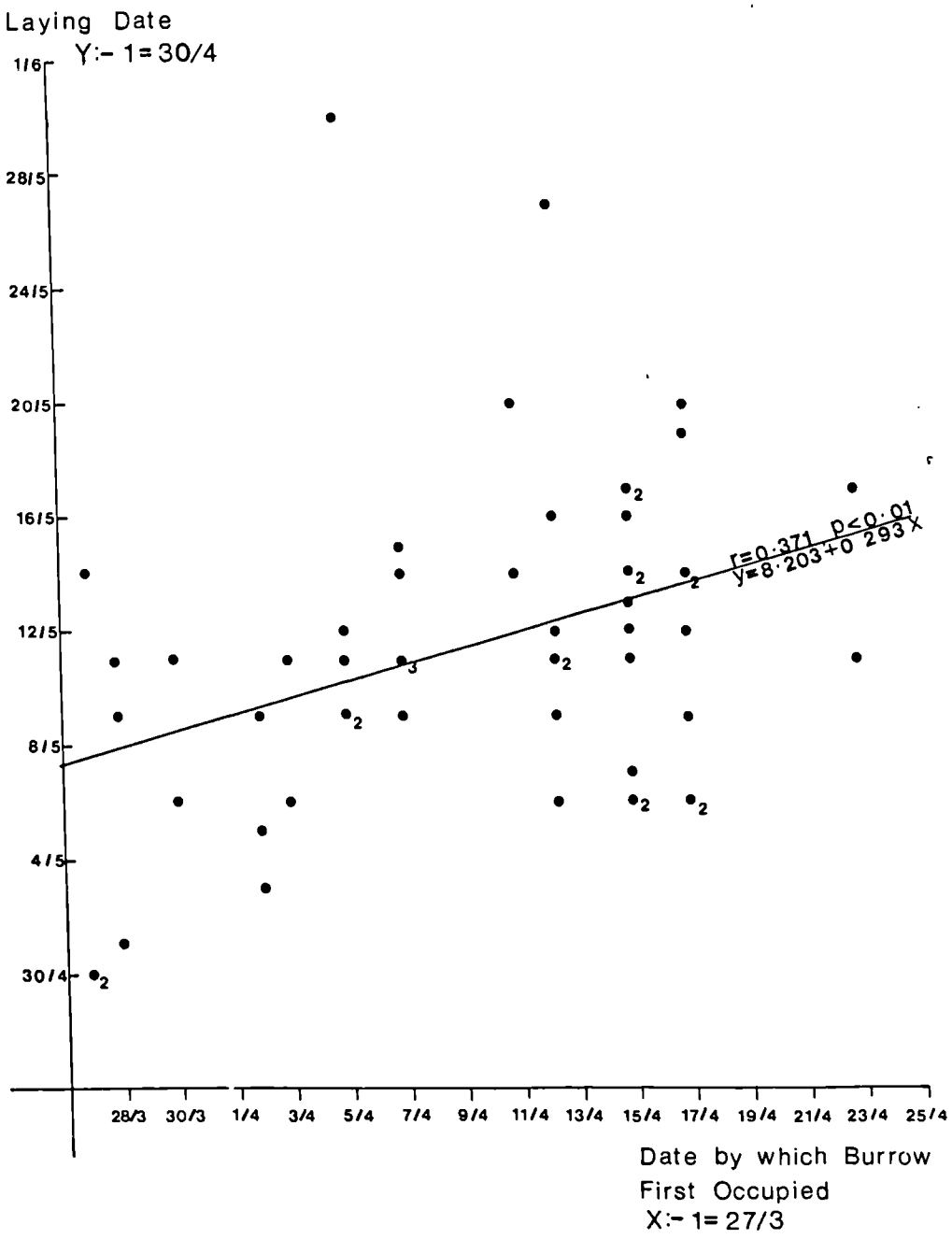


Table 4.3 Laying date (L.D.) in relation to female (F) dimensions.

	1984			1985		
	Sample size	r	p	Sample size	r	p
L.D. vs. F. wing	65	0.009	N.S.	34	0.057	N.S.
L.D. vs. F. bill	58	-0.108	N.S.	34	-0.363	< 0.05
L.D. vs. F. head		-		30	-0.331	N.S.
L.D. vs F. tarsus	35	-0.016	N.S.	32	-0.191	N.S.

Egg size

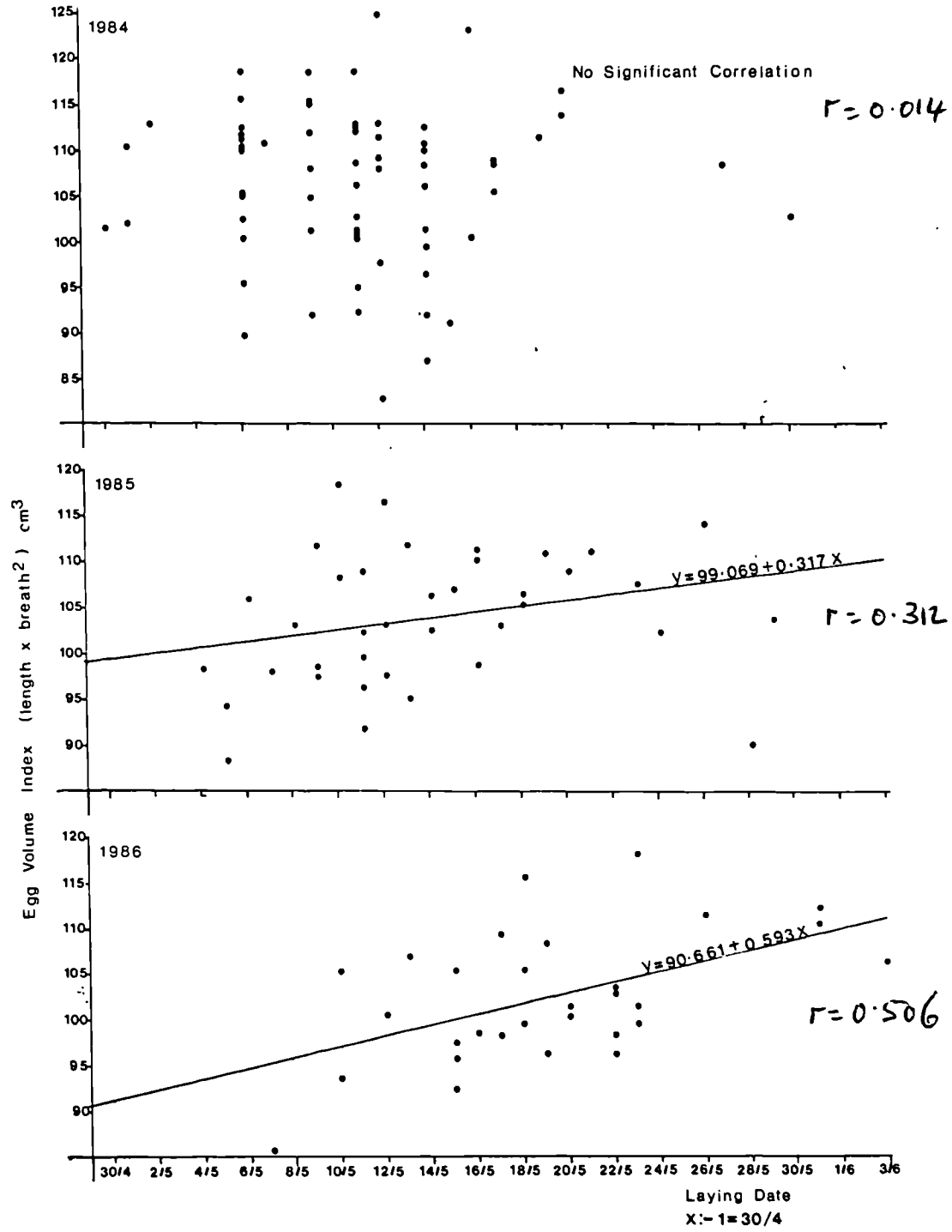
Mean egg volumes in 1984, 1985 and 1986 are given and compared in Table 4.4. There were no significant differences in egg volumes between years.

Table 4.4 Mean egg volume indices (length x breadth^2) in 1984, 1985 and 1986. Figures are cm^3.

Year	No. of eggs	Mean volume index	S.E.	t-test bw. years
1984	68	106.4	1.04	
				t = 1.464, N.S.
1985	43	104.1	1.09	
				t = 0.482, N.S.
1986	33	103.2	1.59	

In many seabirds there is a seasonal decline in egg volume eg Atlantic puffins (Harris, 1980), great skua (Furness, 1983) Brunnich's guillemot, razorbill and black guillemot (Birkhead and Harris, 1985). Brooke (1978a) found that Manx shearwater egg volume tended to decline seasonally in the four years 1973 to 1976 but that this relationship was significant in only one year. Fig. 4.7 illustrates the relationship between egg volume and laying date on Rhum for 1984 to 1986. In the first year there was no seasonal trend, in 1985 there was a tendency for egg size to increase with

Fig. 4·7 EGG VOLUME IN RELATION TO LAYING DATE



laying date (r = 0.312, p = 0.052) and in 1986 this seasonal rise in egg volume was significant (r = 0.506, p < 0.01).

Brooke (1978a) found that egg length to breadth ratio decreases with female age ie. older birds tend to lay rounder eggs. In 1984 and 1985 I found no significant correlation between egg length to breadth ratio and laying date (1984, n = 67, r = 0.110; 1985, n = 39, r = 0.086), while in 1986 there was a positive but not quite significant correlation between these variables (n = 30, r = 0.327, 0.05 < p < 0.10).

As shown in Table 4.5, there was no correlation between egg size and female dimensions in either of the years 1984 or 1985 when sufficient data were available for this analysis. Female condition measured within a day of laying was also unrelated to egg dimensions.

Table 4.5 Egg volumes (E.V.) and egg weights (E.W.) in relation to female (F) dimensions.

	1984			1985		
	Sample size	r	p	Sample size	r	p
E.V. vs F. wing	64	-0.044	N.S.	35	0.144	N.S.
E.V. vs F. bill	58	0.140	N.S.	35	-0.231	N.S.
E.V. vs F. head		-		30	0.035	N.S.
E.V. vs F. tarsus	35	0.202	N.S.	33	0.034	N.S.
E.W. vs F. wing		-		31	0.193	N.S.
E.W. vs F. bill		-		31	0.091	N.S.
E.W. vs F. head		-		27	0.235	N.S.
E.W. vs F. tarsus		-		29	0.268	N.S.
E.V. vs F. condition		-		19	-0.151	N.S.
E.W. vs F. condition		-		19	0.012	N.S.

In 1986 I measured bill lengths and weights of as many newly hatched chicks (ie up to 24 hours old) as possible from my observation burrows. As shown in Table 4.6, chick size and mass at hatching tended to show a positive correlation with egg volume and weight. Insufficient data were available to determine whether chick survival prior to fledging was related to egg size. I found no significant correlation between fledging weight and egg volume (1984, n = 14, r = -0.036, N.S.; 1985, n = 16, r = -0.121, N.S.).

Table 4.6. Correlations between chick bill lengths and weights within 24 hours of hatching and egg dimensions, 1986.

	Egg volume	Egg weight
Chick bill length	n = 16 r = 0.330 N.S.	n = 15 r = 0.462 0.05 < p < 0.10
Chick weight	n = 16 r = 0.486 0.05 < p < 0.10	n = 13 r = 0.540 0.05 < p < 0.10

Incubation periods

Mean incubation periods in the observation burrows in 1984, 1985 and 1986 were 51.1 (n = 15, S.E. = 0.878), 52.7 (n = 24, S.E. = 0.392) and 51.8 (n = 12, S.E. = 0.605) days respectively. In no year was there any significant correlation between incubation period and laying date (1984, n = 19, r = -0.290, N.S.; 1985, n = 24, r = -0.167, N.S.; 1986, n = 18, r = 0.050, N.S.). A positive correlation between incubation period and laying date might be expected if early layers had experienced difficulty in incubating their eggs. The mean rate of adult weight loss during incubation shifts in 1984 was 10.9g/day (n = 117, S.E. = 0.356).

Role of fat reserves carried by fledglings

A seasonal decline in weight at fledging has been observed in several species of seabirds in addition to the Manx shearwater eg. common guillemot (Hedgren, 1979) and puffin (Harris, 1982). In the latter example a seasonal decline was not observed in all years and mean fledgling weights were higher in years when sprats formed a large portion of the chicks' diet.

I have no direct evidence that post-fledging survival of fledglings from Rhum is influenced by fledging weight. However, as stated in the introduction, long term studies on Skokholm have indicated higher survival of heavier fledglings. It might be expected that immediate survival would be affected by individuals' ability to migrate to the species' wintering grounds off the east coast of South America. In the following paragraphs I attempt to quantify this, and to examine the feasibility of fledglings undertaking the 9-10,000km flight on their fat reserves alone.

Details of calculation of potential migration range

1) Preliminary estimate of migration range of a Manx shearwater fledgling using powered flight, following the method detailed by Pennycuick (1975, pp25-29)

The following values were used:-

M_1,	takeoff mass - - - - -	0.470kg (own data, page 47)
b,	wingspan - - - - - - - -	0.780m (Warham 1977)
F,	fuel ratio - - - - - - -	0.255 (see below)
e,	energy content of fat- -	4×10^7J/Kg (Pennycuick 1975)
h,	mechanical efficiency of muscles - - - - - - -	0.23 " " "
k,	induced power factor - -	1.20 " " "
R,	ventilation & circulation factor. - - - - - - - -	1.10 " " "

g, acceleration due to gravity - - - - - - - - - $9.81 ms^{-2}$ " " "

X_1, profile power ratio - - 1.20 " " "

ρ, air density at sea level $1.22 kgm^{-2}$ " " "

Notes:-

Profile power ratio is profile power (ie. power needed to overcome wing drag) ÷ power required to fly at minimum possible speed.

The fuel ratio used assumes that an average fledging of 470g carries 120g of fat and has a lean mass of 350g. This is based on the observation that only 2.6% of a total of 1986 adult weights were less than or equal to 350g.

The following parameters are then derived from those given above:-

X_2, metabolic power ratio = $\frac{6.03\ \alpha\ h\ \rho^{1/2}\ b^{3/2}\ M_1^{(\delta-5/3)}}{k^{3/4}\ g^{5/3}}$

(where α and δ are constants with values 3.79 and 0.723 for non-passerines)

= 0.158

D, drag factor depends on the sum of X_1 and X_2 and is taken from Pennycuick's Table II

= 0.488

$(S_d/A)^{1/2}$, is the area of the disc described by the birds' wings in flight relative to the cross sectional area of the bird's body and is given by:-

$(0.25\ \pi\ b^2/2.85\times10^{-3}\ M^{2/3})^{1/2}$ = 16.654

(L/D)', effective lift:drag ratio is then given by:-

$(D/k^{1/2}R) \times (S_d/A)^{1/2}$ = 6.745

This estimate is then increased by 10F% to take account of changes in (L/D)' during the flight as the bird's mass alters giving a revised estimate of 8.464

Y, the flight range is then given by:-

$$(eh/g) \times (L/D)' \times (\ln\{1/1-F\}) = 2337km$$

This method assumes that powered ie. flapping flight is used throughout and that wind speed is zero, so that airspeed and ground speed are the same. However, the data presented in Table 4.7 indicate that shearwaters use a mixture of flapping and gliding flight. A minimum glide to flap ratio of ca. 2.5 to 1 was observed in calm seas with no swell. In rougher seas, and particularly when a swell was running, as is normal in the open Atlantic, the birds added slope soaring to their rapidly alternating flapping and gliding behaviour, and were observed making very long glides in excess of the periods for which they were in view.

Table 4.7 Observed flight patterns of Manx shearwaters between Mallaig and Rhum.

	Sea conditions	
	No swell, wind 2-3, 0.3m waves.	2-3m swell, wind 6-7, 1.0m waves.
Mean flapping spell duration	1.61s n = 15, S.E. = 0.352	1.34s n = 7, S.E. = 0.202
Mean gliding spell duration (excluding slope soaring)	3.85s n = 14, S.E. = 0.568	3.41s n = 5, S.E. = 1.160
Slope soaring	None	Yes:- 12 - > 30s
Glide:flap ratio	2.4:1	2.5:1 excluding slope soaring, probably at least 10:1 overall.

These data suggest that an estimate of glide to flap ratio over the open sea of 10 to 1 would be reasonable, and probably conservative. To allow for this a second estimate of range based on rates of power consumption was made as described below.

2)Estimate of range on basis of rates of power consumption.

These calculations are based on Pennycuick's (1982) methods for estimating the foraging ranges of various procellariiforms in the South Atlantic. The extension of these calculations to much greater distances, involving more radical changes in the bird's mass, means that the results can serve merely as some indication of the increase in range to be achieved through the use of flap gliding flight and do not represent precise estimates of range.

The basis of this method is to work out rates of fat consumption so that the time for which the bird could remain airborne on its fat reserves may be calculated. This information combined with flight speed provides an estimate of range.

a) Power consumption during gliding flight.

Pennycuick suggests that in gliding flight procellariiforms will consume twice their metabolic power (the mechanical equivalent of basal metabolic rate, B.M.R.).

$$B.M.R. \text{ for non-passerines} = 3.79M^{0.723}$$

$$\text{and metabolic power} = h \times B.M.R.$$

In this instance the bird's mass, M, is taken as the mean of the starting and finishing masses ie.

$$(0.47 + 0.35)/2 = 0.41kg$$

which leads to an estimated metabolic power of 0.398W and hence to estimated power consumption in gliding flight of 0.796W.

b) Power consumption during powered ie. flapping flight.

Pennycuick's (1975) formula for the calculation of the power consumption at minimum power speed (ie. for a bird to fly at that speed at which rate of power usage is minimum) is:-

$$P_{mb} = \frac{0.877(Mg)^{3/2} A^{1/4} k^{3/4}}{\rho^{1/2} S_d^{3/4}} = 2.544W$$

The power consumption at maximum range speed is then given by:-

$$P_{mr} = R \times C \times P_{rb}$$

where C is a constant, in this instance 2.947, determined by the values of X_1 and X_2 (Table II, Pennycuick, 1975)

$$= 8.248W$$

c) Mean power consumption then depends upon the ratio of gliding to flapping flight. At a glide:flap ratio of 10:1 mean power consumption is given by:-

$$((10 \times 0.796) + 8.248)/11 = 1.473W$$

This may then be converted to rate of fat usage through dividing by the work equivalent of fat given by Pennycuick (1982) as $8\times10^6 J/kg$ ie.

$$1.473/8\times10^6 = 0.1842\times10^{-6} kgs^{-1}$$

which implies that 0.120kg of fat would sustain flight for

$$0.120/0.1842\times10^{-6} = 0.651466\times10^6 s$$

d) Flight speed is estimated from Pennycuick's (1975) formula for maximum range speed, V_{mr}:-

$$V_{mr} = \frac{B\ 0.760\ (Mg)^{1/2}\ k^{1/4}}{\rho^{1/2}\ A^{1/4}\ S_d^{1/4}}$$

where B is a constant, in this instance 1.654, dependent upon the values of X_1 and X_2 (Table II, Pennycuick, 1975)

$$= 14.43ms^{-1}$$

Note that this estimate of flying speed is similar to that of between 11 and $16ms^{-1}$ observed by Lockley (1953).

e)Range is then given by the product of flight speed and time ie.

$$Y = 14.43 \times 0.651466\times10^6 = 9400654m = 9401km$$

These results indicate that, at an estimated glide to flap ratio of 10 to 1, an "average" fledgling carrying 120g of fat could fly 9400km and hence reach the wintering area off the east coast of South America on its reserves

without needing to feed en route. The journey would take 7.5 days of continuous flight. These calculations are of necessity rather crude and take no account of either wind speeds or the zig-zag nature of the birds' flight. However, in autumn, when the young birds make this flight, they will be assisted for much of their journey by N.E. trade winds (Perrins et. al., 1973) which should at least compensate for the indirect flight path required by slope soaring.

Given these calculations it would appear that lighter than average fledglings may be unable to fly directly to the wintering grounds, necessitating that they be able to find food on the way in order to survive. By contrast, heavy fledglings may reach South America with reserves to spare and thus have valuable time in which to learn how to locate and capture their prey. It is clearly therefore advantageous for shearwaters to fledge their offspring as heavy as possible, and this is apparently easier to achieve if the chicks hatch relatively early in the breeding season.

Discussion

As Manx shearwaters return to Rhum during March but do not commence laying until May, it would appear that some environmental factor or factors prevent earlier laying. The range in laying dates observed also suggests that environmental constraints are involved, and that individual females are affected to varying degrees. There is some evidence that prolonged snow cover of some nest sites delays laying. However, the large and overlapping ranges in laying dates observed at both early and late snow melt sites, suggest that other environmental factors have a greater influence upon timing of breeding.

Perrins (1966) suggested that food supplies early in the season were insufficient to allow female shearwaters to form eggs, and that it is seasonal improvement in food availability which initiates laying. This hypothesis therefore considers that food supply is both the ultimate and

proximate factor determining timing of breeding. However, Brooke (1978a) suggested that it is the demands of incubation on both parents which has ultimately determined laying dates. According to this theory, it is selectively advantageous to delay laying until food supplies are sufficiently abundant close to the colony to enable off-duty parents to recoup the previous incubation shift's losses in time to return to the colony and relieve the sitting bird. Brooke provides evidence that feeding grounds do indeed move closer to Skokholm over the prelaying and incubation period.

Two reasons which Brooke gave for supporting this rather than Perrins' theory, were the observed constancy of median laying dates and egg volumes on Skokholm from year to year. He concluded that this indicated that it was not seasonal changes in food abundance per se which acted as the proximate determinant of laying dates, as the timing and nature of these changes would be expected to vary from year to year, but rather some exogenous or endogenous factor showing exact annual periodicity.

Aspects of the 1984,1985 and 1986 breeding seasons on Rhum are summarised in Table 4.8. Several features suggest that these three breeding seasons ranged from "good" in 1984 to "poor" in 1986, in terms of the constraints placed on the birds by the environment. Although the timing of egg laying was the same in 1984 and 1985, the seasonal decline in fledging weights was more marked in the second year and average chick growth rates lower (cf. Chp. 5). This suggests a more rapid or more severe decline in food availability over the 1985 chick rearing period than occurred in 1984. The stronger correlation between age and date of fledging in 1985 also implies greater difficulty in provisioning older chicks in 1985. Harris (1966b) reported two years, 1963 and 1964, on Skokholm which appear similar to 1984 on Rhum. In neither year was there any significant seasonal trend in fledging weights or chick growth rates, and Harris concluded that

these were "good" years with no shortage of food in the chick rearing period.

Table 4.8 Comparison of the 1984, 1985 and 1986 breeding seasons on Rhum. Figures in parentheses are standard errors.

	1984	1985	1986
Median laying date	11-13/5	11-13/5	20-22/5
Mean daily spring air temperature	7.05° (± 0.820)	6.69° (± 0.933)	5.87° (± 1.052)
Seasonal trend in weight at fledging	r = -0.206 p = 0.06	r = -0.509 p < 0.001	r = -0.579 p < 0.001
Seasonal trend in age at fledging	+ve p < 0.005	+ve p < 0.001	-
Mean egg volume index	106.4cm³ (± 1.04)	104.1cm³ (± 1.09)	103.2cm³ (± 1.59)
Seasonal trend in egg volume	None	+ve p = 0.052	+ve p < 0.01
Seasonal trend in egg length:breadth ratio	None	None	+ve? p > 0.05 p < 0.10
Mean chick weight growth rate	11.81g/d	10.06g/d	11.40g/d

There is considerable evidence that 1986 was a "poor" year for the shearwaters on Rhum. The significantly later laying date, and the indication that younger females tended to lay later than more experienced birds, imply that environmental conditions during the prelaying period differed from those in 1984 and 1985, and directly affected the birds. There is also a suggestion of a reduction in average egg volume in this difficult season. These observations run contrary to Brooke's (1978a) suggestion of laying date coming under strict and unvarying control. Unvarying, endogenously controlled annual rhythms are observed in some shearwater species, notably the various so-called "mutton" birds of the Australasian region eg. the slender-billed shearwater

(Serventy, 1963). In the Manx shearwater, however, it would appear that some environmental factor exerts proximate control over timing of laying. This could be, as Perrins' (1966) hypothesised, the food supply itself, or some feature of the physical environment to which the shearwaters' prey respond eg. sea surface temperature.

The ultimate factor determining laying date in the Manx shearwater may also be a seasonal change in the abundance of certain foods. As Brooke has pointed out, in a species which very seldom lays replacement eggs, it is important for the adults to be able to synchronise their incubation activities so that the first egg is successfully incubated. If the demands of incubation ultimately determine laying dates, then it might be expected that birds would experience greater difficulty incubating eggs early in the season. Shearwater eggs are resistant to chilling for periods of up to 8 days (Matthews, 1954) and so will hatch even if neglected for part of the incubation period. Such periods of neglect prolong the incubation period as embryonic development is severely curtailed when the egg is cold. However, there was no correlation between incubation periods and laying dates in any of the three years of this study.

I suggest that once Manx shearwaters breeding on Rhum are able to obtain sufficient appropriate food to meet the specific nutrient requirements of egg formation, food supply will not constrain successful incubation. Female shearwaters produce eggs equivalent to circa 15% of their own body weight (Harris, 1966b). During incubation, breeding partners sit on average for 6 days at a time (Harris 1966b) and lose weight at a rate of 10.9g per day (cf. page 54). Croxall (1982) suggests that approximately 45.5% of the weight reduction in procellariiforms during incubation shifts is due to water loss with the remaining 55.5% attributable to the metabolism of fat. On this basis, an incubating Manx shearwater would use up $10.9 \times 0.555 = 6.05$g of fat per day. With an energy density of fat of 9.5kcal g^{-1} (Pennycuick,

1975), birds foraging between incubation shifts would need to amass reserves at the rate of 9.5 × 6.05 = 57.5kcal day^{-1}. The diet results described in the following chapter suggest that the Rhum shearwaters eat more squid and less fish during the pre-laying period than they do during incubation. The estimated calorific requirement of 57.5kcal day^{-1} for replenishment of fat reserves during incubation is equivalent to an intake of 68.0g of squid or 32.7g of herring (Bowes and Church, 1970).

In 1985 and 1986 on Rhum, average egg weight was 58.0g (n = 68, S.E. = 0.57). Petit et al. (1984) found the energy densities of egg contents (ie. excluding the shell) among five species of tropical procellariiforms to range from 1.7 to 2.1kcal g^{-1}. Williams et al. (1982) found the mean shell weight of three species of shearwater to be 7.6% (S.E. 0.66) of total egg weight. Therefore, the total energy content, q, of a 58g egg with a contents energy density of 2.0kcal g^{-1} would be:-

$$2((1.00 - 0.076) \times 58) = 107.2\text{kcal}.$$

Egg formation takes place during the females' approximately 10 day absence from the colony during the "honeymoon" period. Kendeigh et al. (1977) give the daily energetic cost of egg production, M, as:-

$$M = (q \times n)/0.77(n + d)$$

where M is kcal per bird per day

q is total egg energy content in kcal

n is number of eggs laid

and d is the number of days before the first egg is laid.

For a Manx shearwater laying a single egg of 107.2kcal in 10 days, this implies a required average daily input of energy for egg formation of 12.7kcal equivalent to 15.1g of squid or 7.2g of herring. Thus, the average daily total energy demands of egg formation are indeed much less than those for successful incubation and represent a requirement for relatively small additional quantities of food each day.

However, the demands of egg formation are somewhat different from those of replacing depleted energy stores following an incubation shift. Whereas the weight reduction of birds during incubation shifts is due to loss of water and metabolism of fat, eggs are rich in protein and calcium. Williams et al. (1982) found yolk and albumen to represent on average 35.8% (S.E. 0.28) and 56.6% (S.E. 0.94) of total egg weight in three species of Puffinus which would equate to 20.8g of yolk and 32.8g of albumen in a 58g Manx shearwater egg. For nine species of procellariiforms, the mean protein contents of yolk and albumen respectively were 15.8% and 10.4%, equivalent to 3.3g of yolk protein and 3.4g of albumen protein in a Manx shearwater egg of the size and composition described above. Houston et. al. (1983) demonstrated that total yolk weights of clutches produced by lesser black-backed gulls were significantly correlated with the female's protein reserves, as indicated by flight muscle index, but were unrelated to lipid reserves. By contrast albumen weights were unrelated to body protein or lipid reserves. Similarly, studies of small passerines such as red-billed queleas (Jones and Ward, 1979) have indicated that whereas yolk formation is determined by female body reserves prior to ovulation, albumen formation depends solely on food intake between ovulation and laying. The process of egg formation thus demands that females be able to build up high body protein reserves prior to ovulation and to ingest sufficient protein following ovulation to produce the albumen. The period of time over which protein reserves for albumen formation are accumulated in procellariiforms is unknown. Some species apparently have a lag period between completion of yolk formation and ovulation, which may have evolved to enable females to accumulate the reserves required for albumen and shell formation (Grau, 1984). However, even if a Manx shearwater were to ingest all the protein required for albumen formation in a single day, this would require the bird to eat only 20.2g of squid or 19.0g of herring, which is

again much less than the daily food requirement to replenish fat reserves lost during incubation shifts. It would therefore appear that neither the energetic costs or protein demands of egg formation in the Manx shearwater are sufficient to prevent laying earlier in the season than is observed. These calculations tend to support Brooke's theory rather than Perrin's.

Another possibility is that the requirement for calcium to form the eggshell might be the ultimate limiting factor which has determined the laying date *of Manx* shearwaters on Rhum. The calcium for egg shell formation in birds may either be derived directly from the diet in the period between ovulation and laying, or from labile reserves in the medullary bone which is formed in females one or two weeks prior to reproduction (Simkiss, 1975). The relative importance of these two sources of calcium during eggshell formation in shearwaters is unknown. However, the total calcium requirement for shell formation, whether derived directly or indirectly from the diet, is high in relation to the concentrations of calcium present in some of the food items exploited by Manx shearwaters. The weight of calcium in a 4.4g shell (58 x 0.076, page 64) composed of calcium carbonate would be 1.76g. In order to obtain this quantity of calcium a shearwater would need to consume over 14.7kg of squid, equivalent to 216 times the daily intake required to recoup incubation shift energy reserves (cf. page 64). Bony fish contain much greater concentrations of calcium than do invertebrates such as squid. Assuming that the skeleton comprises on average 2% of the total weight of a teleost fish (Vinogradov, 1953) and that calcium makes up 39% of the skeletal weight (Prosser, 1973), a shearwater would require only 225g of fish to obtain sufficient calcium for eggshell formation. At the rate of intake of 32.7g of fish per day required to replace energy rerves lost during incubation shifts (cf. page 64), sufficient calcium for shell formation could be ingested in just 7 days. This is similar to average

incubation shift duration. These calculations suggest that once fish is sufficiently available to enable egg formation, the Rhum shearwaters should not experience any difficulty in obtaining sufficient food for successful incubation. Given that the demands of eggshell formation and incubation appear to place similar dietary intake demands upon Manx shearwaters, it is unclear as to which may ultimately have determined timing of laying. However, in view of the relatively low calcium requirement for egg formation in relation to a female shearwater's skeletal calcium reserves, it might be hypothesised that Brooke is correct in his suggestion of timing of laying having been ultimately determined by the demands of incubation, but that the proximate control is exerted through the availability of calcium in the form of fish. The evolution of a mechanism whereby female shearwaters derive the calcium for eggshell formation directly from their diet in the honeymoon period would effectively prevent laying before successful incubation could occur. Such a mechanism would also account for the observed inter-annual differences in timing of laying, and the lack of any indication of early layers experiencing any greater difficulty than late birds in incubating their eggs. Studies of the physiology of female shearwaters and of changes in the availability of fish during the pre-laying period would be required to confirm or refute this hypothesis.

As stated above, studies of Manx shearwaters to date have indicated that, in those years when egg volume shows any seasonal trends, the tendency is for later eggs to be smaller (Brooke, 1978a). It has already been shown that early breeding enhances the chances of fledging viable chicks. By contrast there is no relationship between fledging weight, and hence probability of survival, and egg volume (cf. page 54; Brooke, 1977). It would therefore be expected that females should lay earlier rather than delay laying in order to produce a larger egg. Birkhead and Nettleship (1982) have

demonstrated quantitatively the selective advantage to Brunnich's guillemot females in laying as early as possible rather than forming larger eggs despite the positive correlation between fledging weight and egg volume in that species. In view of previous observations and theoretical considerations, the observed rise in egg volume over the laying period in 1985 and more especially in 1986 is unexpected.

One possible explanation for the positive correlation between egg volume and laying date observed in 1986, could be that food availability, rather than improving gradually, showed a more stepped or sudden increase. In this situation the most proficient, perhaps older, females would be able to produce small eggs early in the season prior to the rather sudden improvement in food supply. Less proficient, perhaps younger, birds would be unable to form eggs until after the hypothesised stepped increase in food availability had occurred. Some evidence that there may have been a sudden increase in food availability in 1986 is provided by the meteorological data described above. Air and sea temperatures in April and early May were lower than normal so that the sea's productivity would have been depressed below average for that time of year. This would make it more difficult for the shearwaters to accumulate the reserves needed for egg formation during the normal "honeymoon" period. In addition, May 1986 was generally windier than normal, and in particular there were three days of continuous gales just prior to the 1984 and 1985 laying peak of ca. 11th May (pers. obs.). The subsequent reduction in the frequency of strong winds, and hence heavy seas, would have resulted in a rise in food availability to birds previously hampered in foraging by the sea conditions. The generally stormy pre-laying period in 1986 might also have reduced food abundance by delaying the formation of the productive frontal systems described in Chapter 2. Also, as sea temperatures by late May were apparently approaching the

seasonal norm, prey abundance would probably have been greater than during the usual "honeymoon" period in late April/early May. Several studies have indicated that whereas yolk size does not increase proportionately with overall egg volume, larger eggs contain relatively more albumen (Nisbet, 1978). If, as suggested above, albumen size is determined by dietary intake between ovulation and laying, then later laying birds in a season in which food supply tended to show a stepped rather than steady increase, might be expected to produce larger eggs as they would ovulate in a period of relative abundance of food. This would also explain the apparent trend in 1986 for younger birds to lay later and larger eggs. Inexperienced birds would be those most likely to have been prevented, by rough sea conditions and generally reduced prey abundance, from building up reserves for egg formation at the normal time. Unusually high food availability, as compared to that in normal years during the usual "honeymoon" period, would have enabled these inexperienced birds to produce unusually large eggs once feeding conditions had improved.

While there is apparently no sustained advantage to Manx shearwaters in producing large eggs, chick mass at hatching is correlated with egg size. This is likely to enhance chick survival immediately post-hatching particularly if parents are for any reason unable to feed the chick immediately. Increased survival among young chicks hatched from relatively large eggs has been demonstrated in several species eg. kittiwake (Thomas, 1983), common and roseate terns (Nisbet, 1978). Thus in a situation where food is abundant in the egg formation period, so that rates of egg formation approach physiological maxima, there may be a selective advantage in laying as large an egg as possible on a given date.

Chapter 5

FEEDING ECOLOGY AND CHICK GROWTH

Introduction

Food availability and dietary composition are clearly of vital importance to any organism's survival and reproduction. As discussed in Chapter 2, the marine productivity of the Hebridean area during the summer months is enhanced by the formation of fronts between water masses of differing salinity and origins. The richness of these areas is cited as a contributory factor to the diversity and size of seabird breeding colonies within the Hebrides (Bourne and Harris, 1979). Clearly, however, even within such a highly productive ecosystem, there will be year to year variations in food availability, and in addition individual birds of any one species will differ in their ability to exploit the resources available. In this chapter I seek to investigate such variations as well as to present a general account of the diet and chick growth of the Manx shearwaters on Rhum.

A) Adult and chick diets

Methods

Information on diets was derived from three sources:

(1) Adult regurgitates:-

Adult Manx shearwaters coming into the colony at night to feed young sometimes regurgitate food when handled. Such regurgitates provide qualitative information on chick diet.

(2) Samples of adult proventricular contents obtained by use of a stomach "pump":-

Even during the chick rearing period many adults do not regurgitate food when handled so that other methods were necessary to obtain larger numbers of samples and to examine adult diet at other times.

The use of emetics is fraught with difficulties as such techniques essentially involve administering carefully measured doses of poison at such concentrations as will cause vomiting without adversely affecting the bird. Tartar and digitalis emetics have been most frequently tested but the majority of trials have highlighted the difficulties involved in balancing effective and consistent emesis against increased mortality (Lederer and Crane, 1978; Zach and Falls, 1976). In attempting to sample the stomach contents of larger non-passerines, further problems may arise from the absorption of emetic by stomach contents preventing immediate emeseis while allowing slow, and prehaps fatal, absorption of the poison into body tissues (Croxall and Prince, 1980).

A safer alternative to the use of emetics is to pump or flush out proventricular contents. In order to sample Manx shearwater diets I used a slightly modified version of the device employed by Randall and Davidson (1981) for Jackass penguins. This technique involves inserting a rigid plastic tube into the bird's stomach and pumping water in via a smaller tube placed inside the first. Once water is seen to rise up inside the outer tube, the inner tube is removed and the bird held upside down over a container so that the water and stomach contents run out through the original tube. No immediate mortalities resulted from the use of this device and none of the birds sampled were subsequently found dead. Of 7 birds found and stomach flushed along the regularly traversed observation transects, 5 were subsequently recaptured. While none of the 36 birds sampled elsewhere were subsequently recovered, neither were any of 19 handled, but not stomach pumped, on the same dates and in the same

areas as those from which samples were obtained. It may be concluded that the low overall recapture rate among stomach flushed birds arose from infrequency of visits to these areas rather than from high mortality. In common with the collection of regurgitates, this method samples proventricular contents only. There are several inherent biases associated with this technique:-

(a) Intact items of a diameter greater than the bore of the outer tube (9.5mm) will not be sampled.

(b) As the entire contents of the proventriculus may not be removed, any tendency for different food items to become separated into distinct zones within the stomach may bias the samples obtained (Volkman et al., 1980).

(3) Dissection of intact corpses found in the shearwater colony:-

The majority of these were adults which had fatally injured themselves in landing at the colony. Few chicks were included in this sample as chick survival was generally very high, and only a small number were accessible to me in the observation burrows. Samples collected in this way complemented those obtained as described above, as gizzard contents were available in additon to material from the proventriculus.

All food samples were preserved in 70% alcohol prior to laboratory examination. As the majority of the samples collected could not be taken as necessarily representing the entire stomach contents of the birds from which they were collected, no attempt was made at quantitative analysis of diet. Even complete stomach contents may provide a biased picture of diet where a variety of food items differ in the speed at which they are digested and in the persistence of associated hard parts in the gizzard (Swanson and Bartonek, 1970; Brown et al., 1981). However, these samples do provide useful qualitative information on the range of items exploited by the Rhum shearwaters. In the laboratory the

samples were first washed in a 0.5mm sieve to remove oil and particles of solid material too small to be of use in identification. Large, relatively intact, items were separated out and measured, and the remaining material was then examined under a binocular microscope at 6 to 25 times magnification. Cephalopod beaks and fish otoliths were removed, and remaining soft parts identified to the lowest taxonomic status possible (Muus & Dahlstrom, 1977). Most of the cephalopod beaks were very abraded but where possible they were identified by Dr. M. Imber of the New Zealand Wildlife Service. Otoliths were identified by comparison with Dr. A. V. Hudson's reference collection from marine fish around Shetland.

Results

The results are summarised in Tables 5.1. and 5.2. There was no difference in the frequency of occurrence of fish and squid in the proventricular samples collected in 1984 and 1985 (χ^2 = 0.143, d.f. = 1, $p > 0.10$) so the data from both years were pooled. Identification of fish proved difficult as many of the samples were highly digested and lacking any bones. Even the more intact samples were generally headless so that otoliths were present in only 4 of the 47 samples in which fish flesh was identified. Essentially it was possible only to distinguish between relatively intact sandeels and similarly undigested sprats/young herring on the basis of the position of the spine within the body. Many of the less digested samples contained spinal sections of 10-30mm in length suggesting that the original fish were 50mm or longer. The largest intact fish in the samples was a sprat measuring 80mm long by 17.5mm maximum depth.

Comparison of proventriculus with gizzard contents (Table 5.1) illustrates the bias towards squid in gizzards, as squid beaks are often the only dietary component which can

Table 5.1 Results of stomach contents analysis (data for 1984 and 1985 pooled)

Type	No. of samples	No. with food	Percentage of stomachs with food which contained: Squid	Sandeel	Sprat/ herring	Other fish	Fish sp. unknown	Total fish	Crustacea	Fish & squid
Adults in pre-laying period:-										
P	13	11	81.8%	0%	0%	9.1%	45.5%	54.5%	0%	27.3%
G	4	3	100%	0%	0%	0%	66.7%	66.7%	0%	66.7%
Adults in incubation period:-										
P	25	17	52.9%	5.9%	5.9%	0%	47.1%	58.8%	17.6%	11.8%
G	6	0	-	-	-	-	-	-	-	-
Adults in chick-rearing period:-										
P	37	34	11.8%	23.5%	26.5%	0%	52.9%	91.2%	8.8%	5.9%
G	3	2	100%	0%	0%	0%	0%	0%	0%	0%
Chicks:-										
P	3	3	100%	33.3%	0%	0%	0%	33.3%	0%	33.3%
G	3	1	100%	0%	0%	0%	0%	0%	0%	0%
Fledglings:-										
P	5	0	-	-	-	-	-	-	-	-
G	5	5	100%	0%	0%	0%	0%	0%	0%	0%

Notes:

(1) P = proventriculi; G = gizzards (dissected samples only)
(2) Other fish:- the only identified species found was sheppy argentine.
(3) Fish & squid is percentage of stomachs in which fish and squid remains occured together and includes samples already placed in the individual fish and squid columns.

withstand digestion in the proventriculus plus physical abrasion in the gizzard itself. Conversely, squid flesh is apparently more rapidly digested than fish, so that proventricular contents analysis is biased towards over-representation of fish.

Small crustaceans were found in a few of the stomachs examined, but only in association with well digested fish remains so that it is likely that they were derived from fish stomachs rather than being eaten directly by the shearwaters.

Of the 37 squid beak fragments examined by Dr. Imber 17 were too worn to be identified. The remaining 20 were identified as shown below in Table 5.2. These data indicate that Ommastrephidae spp. were the squid most commonly exploited by the shearwaters. The species included are not themselves bio-luminescent but the shearwaters may be able to detect their disturbance of bio-luminescent plankton swarms when they move towards the surface at night (Imber and Berruti, 1981). The other squid found in the samples are bio-luminescent as is the sheppy argentine fish identified from one sample in the pre-laying period.

In summary, it appears that adult Manx shearwaters on Rhum feed predominantly on a mixture of small squid, particularly juvenile Ommastrephidae, and fish up to 80mm long including sandeels and sprats or juvenile herring. The proportion of fish in the diet apparently increases during the chick rearing period.

Table 5.2 Cephalopod species identified from Manx shearwater stomachs, Rhum 1984 and 1985

Family	Species	Age	Number	Characteristics (Herring, 1977)
Ommastrephidae	Any or all of:-	J	14	
	Todarodes sagittatus			Upper mesopelagic or epipelagic, not luminescent, migrate to sea surface at night.
	Illex coindetii			
	Todaropsis eblanae.			
Cranchiidae	*Teuthowenia megalops*	I	1	Luminescent
	Taonius pavo	A	1	
Gonatidae	*Gonatus steenstrupi*	A	2	Luminescent
Onychoteuthidae	*Onychoteuthis banksii*	A	1	Upper mesopelagic or epipelagic, luminescent
Mastigoteuthidae	*Mastigoteuthis* sp.	A	1	Lower mesopelagic and luminescent

Notes:
J = juvenile
I = immature
A = adult

B) Chick feeding and growth

Methods

In 1984 and 1985 the observation burrows were checked regularly at 1-2 day intervals during the hatching period. As the eggs took over 24 hours to hatch from first pipping, this allowed hatching dates, and hence chick ages, to be assessed.

In 1984, 17 chicks from the observation burrows survived to fledge and were weighed on 55 days between 23rd June and 25th September. This included 35 instances of weighings being made on two consecutive days, thus providing estimates of net daily mass increments. Bill length measurements were also made. In addition, feed sizes were estimated by 2 or more weighings of the chicks on 13 nights, following the methodology of Ricklefs (1984).

In 1985, 20 chicks from the observation burrows survived to fledge. Wet weather during the chick rearing period restricted weighings of these to 33 days between 27th June and 25th September. Bill and wing lengths were also measured on these occasions. Weighings on consecutive days were possible on only 5 occasions and feed sizes were estimated directly on 8 nights.

In both years chicks of less than 300g were weighed to the nearest 1g and thereafter to the nearest 5g. Wing measurements were to the nearest mm and bill lengths to the nearest 0.1mm.

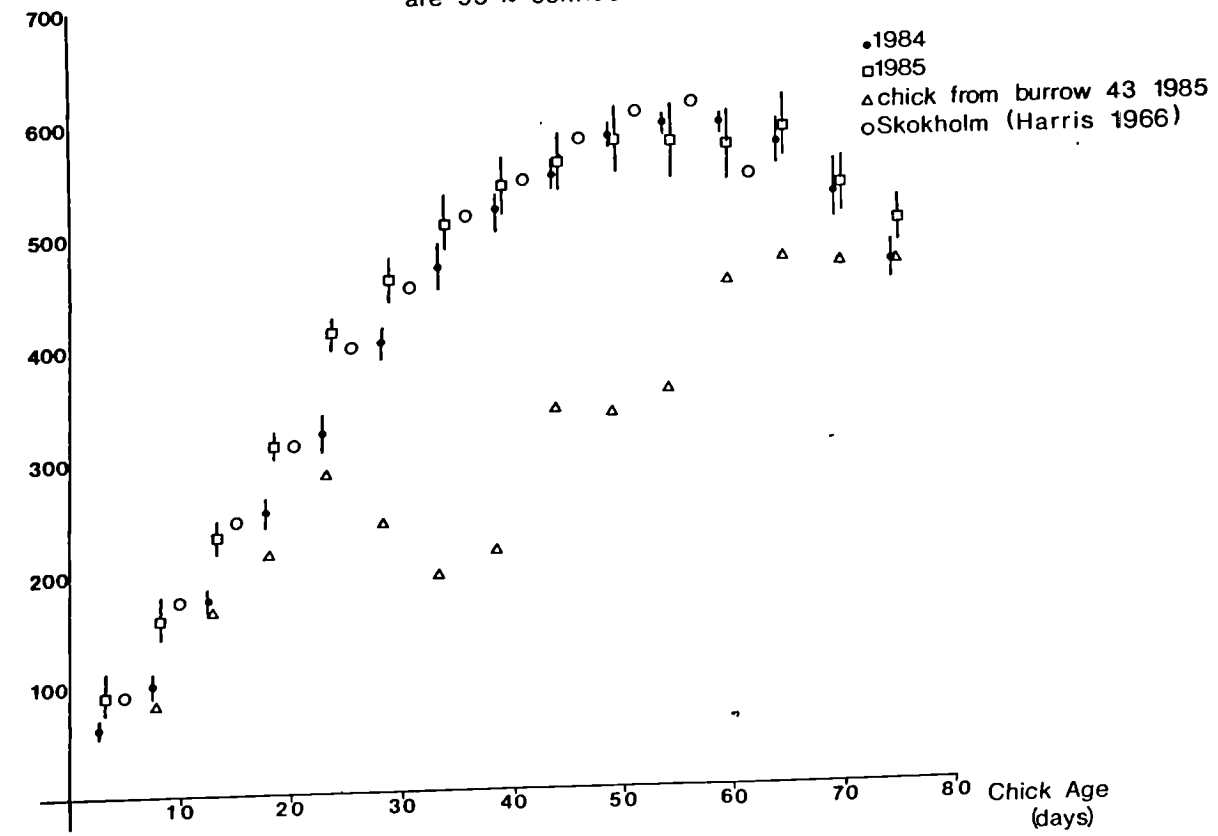
Results

Chick growth

Average weight increase curves for 1984 and 1985 are given in Fig. 5.1. The form of these curves is typical of procellariiform species with rapid growth to a peak weight in excess of adult weight followed by a period of weight loss prior to fledging (Harris, 1969). An index of growth rate, defined as the slope of the best fit linear regression line of mass against age up to day 50, during which period weight

Fig. 5·1 CHICK WEIGHT GROWTH

Each point is the average weight over all chicks for the 5 day age classes indicated. Vertical lines are 95 % confidence intervals

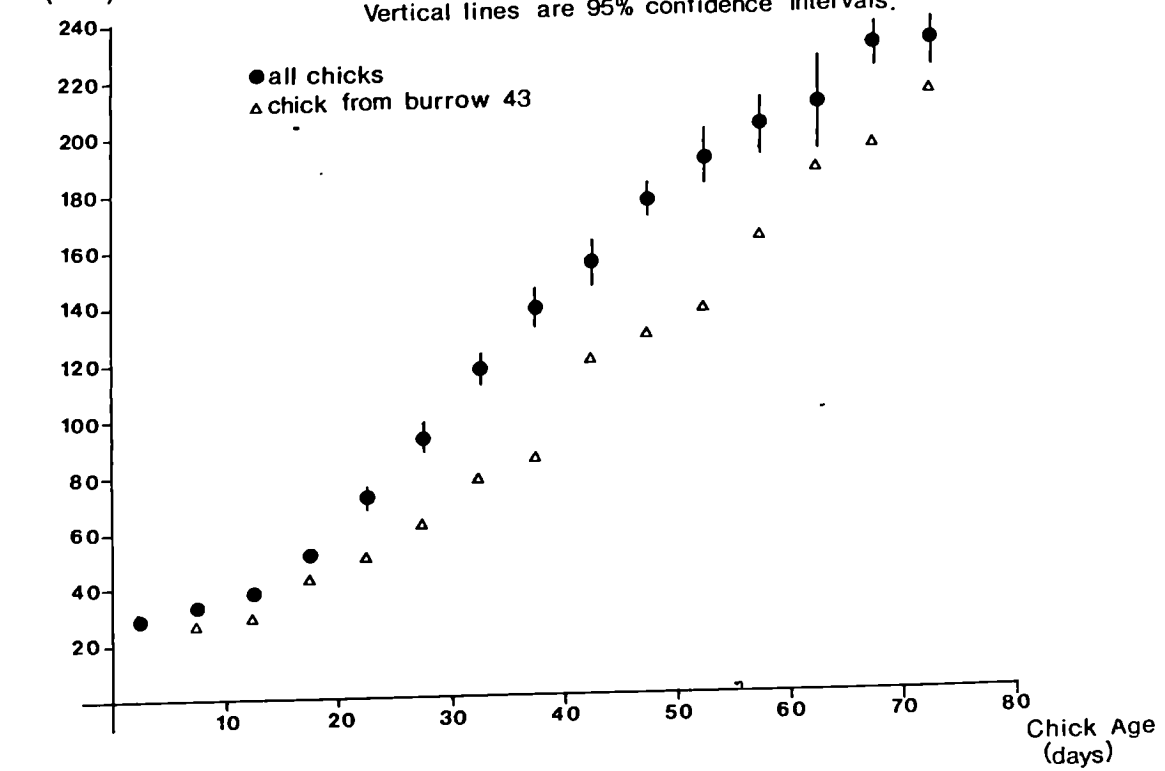


gain is approximately linear (cf. Fig. 5.1), was used for comparison between individuals and years. In 1984 this had a mean of 11.8g/day (S.E. 0.39) while in 1985 the mean of 10.1g/day (S.E. 0.57) was significantly lower ($t = 2.433$, d.f. = 35, $p < 0.05$). Average bill growth rates were also significantly lower in 1985 (1984, mean = 0.41mm/day, S.E. = 0.005; 1985, mean = 0.37mm/day, S.E. = 0.011; $p < 0.001$, Fisher-Behrens test). The variance in weight of chicks was generally higher in 1985 with $p < 0.05$ (F-test) at all ages excepting 21-25 and 71-75 days. This was in part due to the very abnormal growth of two chicks in 1985. Both of these chicks were left alone in their burrows and not fed for periods of many days at a time. The weight and wing growth curves of one of these chicks, from burrow 43, are shown in Figs. 5.1 and 5.2. However, the overall reduction in growth rates in 1985 was not solely due to these chicks. A comparison of growth rates of chicks in the 7 burrows from which chicks fledged in both years also indicates significantly reduced rates in 1985 (1984, mean = 12.22g/day, S.E. = 0 18; 1985, mean = 10.03g/day, S.E.= 0.83; $p < 0.05$, Fisher-Behrens test for comparison of samples with unequal variances).

Figure 5.1 illustrates that while mean growth rate up to 50 days was lower in 1985, chicks up to 30 days of age were heavier than in 1984. This arose from the greater average early weight of chicks in 1985 with a mean 1-5 day weight of 90.9g (S.E. 9.37) as compared to 62.4g (S.E. 3.82) in 1984 ($p<0.05$, Fisher-Behrens test). There was, however, no indication that the surviving 1985 chicks hatched from larger eggs than their 1984 counterparts.

The 1985 wing growth curve shown in Fig. 5.2 illustrates that feather growth, in contrast to weight increase, continues right up to fledging and indeed beyond (Brooke, 1977). The implications of this are discussed later.

Fig. 5·2 CHICK WING GROWTH 1985
Each point is the average wing length over all chicks for the 5 day age classes indicated. Vertical lines are 95% confidence intervals.

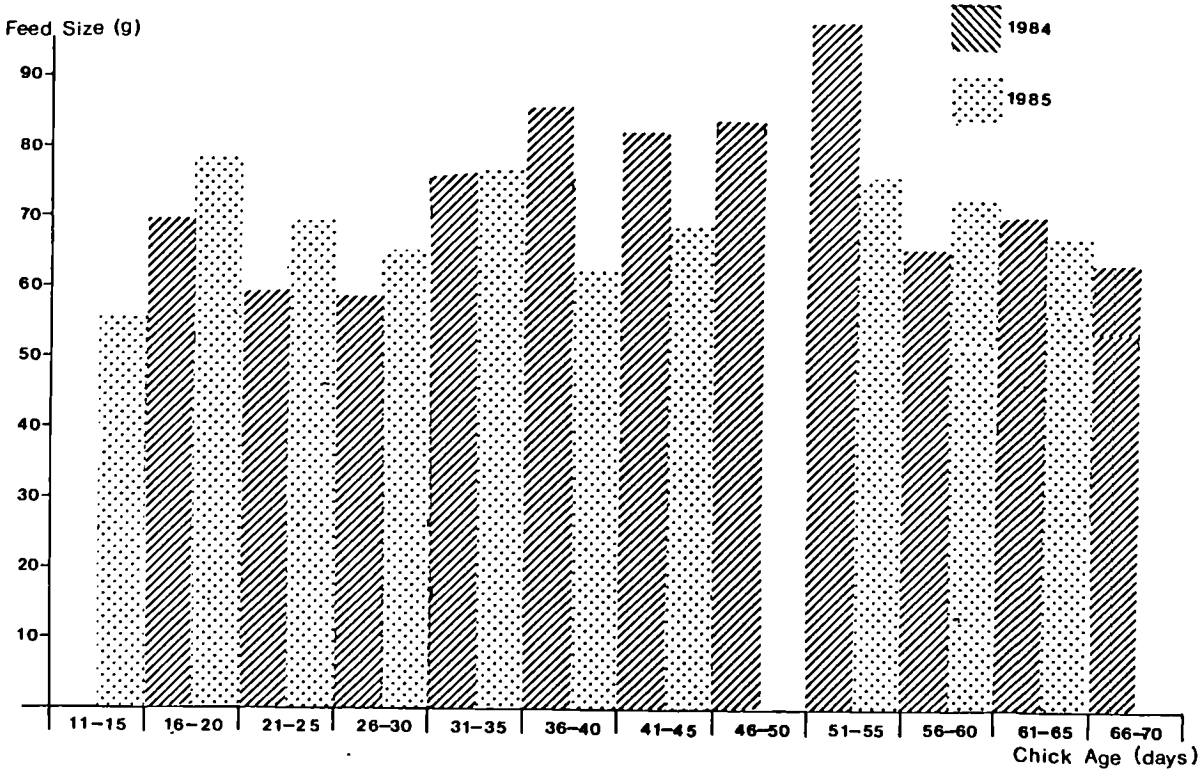


Feed sizes

Estimated average total feed sizes for different age classes of chicks in 1984 and 1985 are given in Fig. 5.3. These figures were derived from chick mass increments obtained by weighing chicks at intervals of between 3 and 8 hours during the hours of darkness when feeding occurs. The total mass increase in a single night is the sum of all positive mass increments recorded during that night. As rates of chick weight loss due to respiration and defaecation are greater in the period immediately after feeding than in the early part of the night just prior to feeding, the measured mass increase underestimates true feed size (Ricklefs et al., 1985). The extent of this bias may be estimated by averaging pre- and post-feed weight loss rates over the time interval at which chicks were weighed.

During two 24 hour periods in 1984 (24-25/8 and 31/8-1/9), the 17 chicks surviving in the observation burrows were weighed every 4 hours. On the first occasion, the mean age of the chicks was 54 days (S.E. 1.18) while the mean starting weights on each occasion were 590.3g (S.E. 15.89) and 564.7g (S.E. 10.23) respectively. Analysis of these data provided estimates of weight loss rates in the 4 hour periods immediately prior to, and immediately after, feeding of 2.2g/hr and 4.9g/hr respectively. These loss rates indicate a shortfall of 14.2g in feed size estimate over a 4hr period, assuming that feeds were randomly distributed throughout the 4hr period over which mass increment was estimated. Therefore, in estimating feed sizes for 1984, when the average interval between weighings was 4.2 hours, 15g has been added to the observed mass increments which were originally measured to the nearest 5g. In 1985, the average interval between night time chick weighings was 6.9 hours. Using the same data as above, average loss rates in 8 hour periods before and after feeding were calculated as 1.7g/hr and 4.0g/hr respectively indicating a bias of 23.1g over an 8 hour period, so that 20g have been added to the mass

Fig. 5·3 AVERAGE CHICK FEED SIZES



increments observed in 1985 to obtain the feed size estimates shown.

Average feed sizes of chicks in age categories 11-30 days, 31-55 days and 56-70 days in 1984 and 1985 are given and compared in Table 5.3. In 1984, feed sizes were significantly higher for chicks aged 31-55 days than for older or younger chicks, whereas in 1985 there was no apparent change over the chick rearing period. There were no significant differences in feed sizes between 1984 and 1985.

Table 5.3 Mean feed sizes (± S.E.) for chicks of different age classes in 1984 and 1985. Sample sizes in parenthesis. Probability values, p, from t-tests.

Age	p between ages, 1984	1984	p between years	1985	p between ages, 1985
11-30 days		60.35 ± 5.982 (20)		68.50 ± 3.318 (66)	
	p < 0.01		N.S.		N.S.
31-55 days		84.84 ± 3.632 (93)		72.36 ± 5.081 (36)	
	p < 0.001		N.S.		N.S.
56-70 days		66.07 ± 3.516 (61)		67.33 ± 10.315 (15)	
			N.S.		
All ages		75.44 ± 2.511 (174)		69.54 ± 2.749 (117)	
			N.S.		

Feeding frequency

The frequency distributions of night time chick mass increments in 1984 and 1985 are shown in Figure 5.4. These data may be used to estimate chick feeding probabilities as described below (from Ricklefs, 1984):-

If the probability that an adult bird will feed its chick on any given night is P, then the probability that it will not feed the chick is 1-P. Assuming that parents act independently, it follows therefore that the probability of neither parent feeding a chick is $(1-P)^2$ and this may be estimated from the observed frequency of zero or negative mass ~~increments~~ changes. In 1984 these represented 15.1% of all 206 recorded mass ~~increments~~ changes ie $(1-P)^2 = 0.151$ so that $1-P = 0.388$ and $P = 0.612$. Further, the probability of both parents feeding their chick on one night is P^2; in this case 0.375. Averaging the highest 37.5% of observed mass increments gives a mean of 89.8g, equivalent to an actual feed size of 104.8g (n = 77, S.E. = 3.19) or 25.3% of adult weight. Similarly, the mean single feed size of 51.8g (n = 98, S.E. = 1.12), or 12.5% of adult weight, was estimated from the average of all positive mass increments excluding the top 37.5%. Note that the estimated mean double feed size is almost identical to twice the single feed mean.

In 1985, $(1-P)^2$ was estimated as 0.250, corresponding to a value for P of 0.500. The average mass increment for the highest 25.0% ($= p^2$) of cases was 83.3g leading to an estimated mean double feed size of 103.3g (n = 39, S.E. = 3.63), equivalent to 25.0% of adult weight. Similarly the mean single feed size was estimated as 52.6g (n = 78, S.E. = 1.65), or 12.6% of adult weight which again is very close to half the calculated mean for double feeds.

From the results so far described, it appears that the size of feeds brought to chicks did not vary significantly between 1984 and 1985. However, as shown in Table 5.4, the probability of being fed on a given night was greater in 1984 than in 1985. The overall probabilities of

Fig. 5·4 MASS INCREMENT FREQUENCY DISTRIBUTIONS

Fig. 5·4a 1984

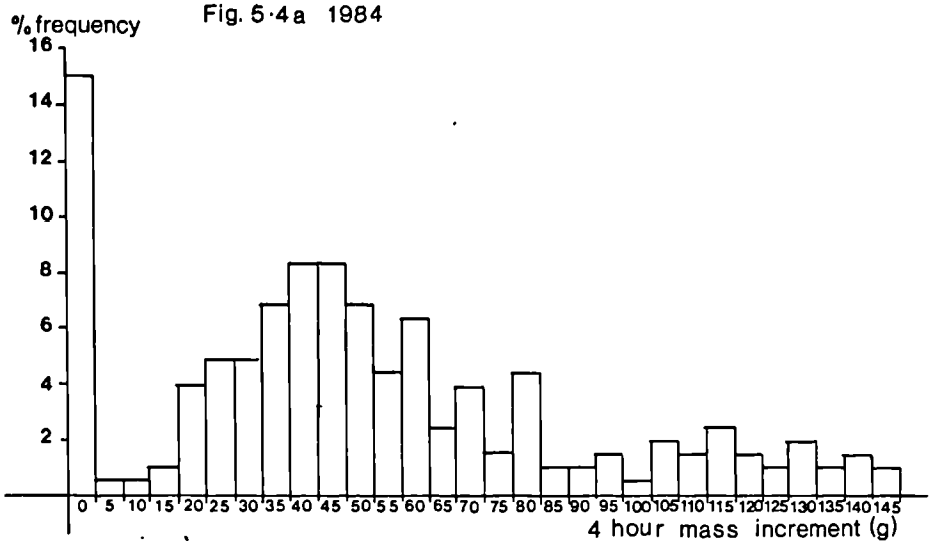
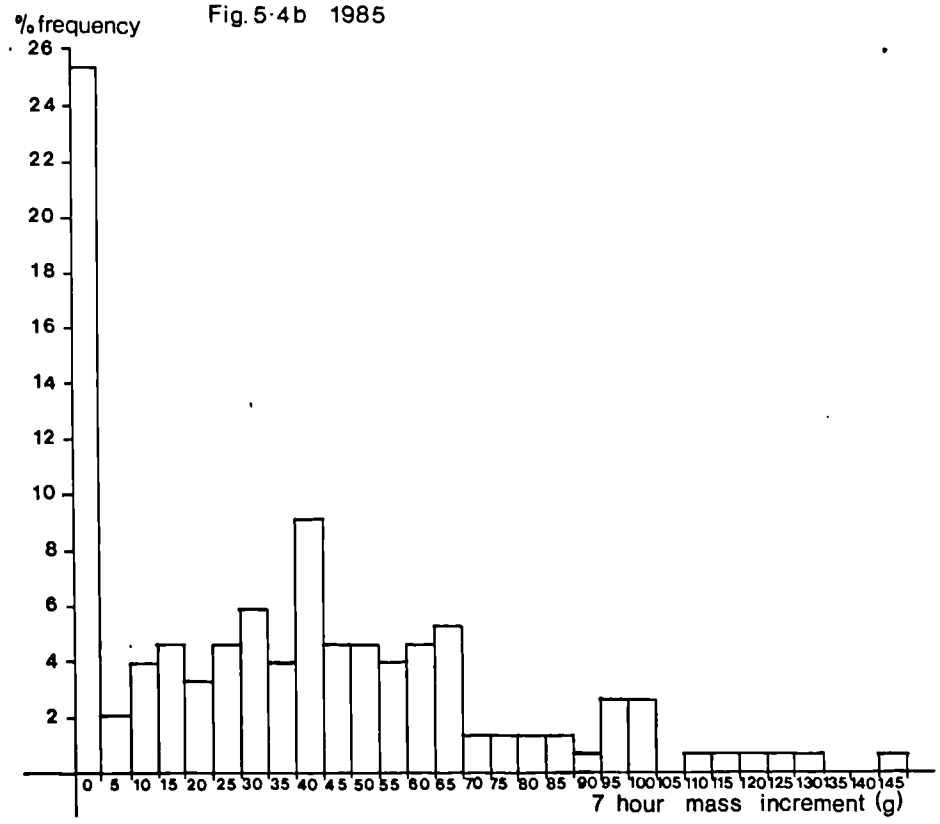


Fig. 5·4b 1985



being fed, whether by one or both parents, corresponded to feeding intervals of 1.18 days and 1.34 days in 1984 and 1985 respectively. This suggests that feeding grounds may have been closer to the colony, or more predictable in their location, in 1984.

Table 5.4. Chi^2 analysis of feeding probabilities in 1984 and 1985.

O = Observed single feed equivalents ie. observed frequency of single feeds + 2(observed frequency of double feeds)
E = expected frequencies

Year / Feeds	1984	1985	Totals
Single feed equivalents	O = 252 E = 241	O = 153 E = 164	405
Zero feeds	O = 31 E = 42	O = 39 E = 28	70
Totals	283	192	475

$\chi^2 = 8.441$, d.f. = 1, $p < 0.01$

Variations in feeding frequency with chick age

The frequencies at which different age classes of chicks were fed in 1984 are shown in Table 5.5. In compiling this table it has been assumed that positive mass increments of less than 60g represent feeding by one parent while those of 60g or over indicate feeding by both parents. The p_i values represent the proportions of the potential feeds (ie. 2 per chick per night) which were actually delivered. In order to compare feeding frequencies between age classes, it is necessary to transform these observed proportions to corresponding angles, θ_i, where $\theta_i = \sin^{-1}(p_i)^{1/2}$. These may

then be compared with the overall value of θ for the entire sample, θ_t, according to the formula:-

$$Z = \frac{\theta_i - \theta_t}{S.D.\ \theta_i}$$

where S.D. $\theta_i = (820.7/n_i)^{1/2}$ and n_i is the number of parents in case i. In a binomial distribution Z has a mean of zero and S.D. of 1. In this instance the observed distribution departs significantly from the binomial, indicating considerable variation in feeding frequency among different age classes of chicks. Examination of the individual Z scores indicate high feeding frequencies in chicks aged 41-55, with a very marked decline from 61-70 days as chicks approach fledging. In addition to this reduction in the frequency of feeds brought to chicks near fledging, the results presented in Table 5.3 indicate that feed size also declined at this time in 1984.

Table 5.5 Variation in feeding frequency with chick age in 1984.

Age	n_i	No. Feeds 0	1	2	p_i	θ_i	Z	
21-25	16	3	4	1	0.375	37.76	-1.678	
26-30	18	0	6	3	0.667	54.76	+0.738	
31-35	26	3	4	6	0.615	51.65	+0.333	
36-40	26	5	3	5	0.500	45.00	-0.851	
41-45	40	1	9	10	0.725	58.37	+1.896	
46-50	54	3	10	14	0.704	57.04	+1.862	
51-55	54	2	10	15	0.741	59.41	+2.470	*
56-60	66	1	23	9	0.621	52.00	+0.630	
61-65	56	9	15	4	0.411	39.87	-2.589	*
66-70	30	9	5	1	0.233	28.86	-4.000	**

$\bar{n}_i = 38.60$ $\quad \bar{\theta}_i = 48.47$ $\quad \bar{Z} = -0.119$

Var = 104.28, S.D.= 2.117

With a mean n_i of 38.60 the expected variance in θ_i is 820.7/38.60 = 21.262.
The ratio of the observed variance (104.285) to the expected is significant ($F = 4.905$, $p < 0.05$).

Notes:-
* = Z significant at 5% level
** = Z significant at 1% level

Variations in feeding frequency between nights

The same analysis as described above was also used to compare feeding frequencies on 13 nights in late July and August 1984. Data from later in the breeding season were not included as the previous analysis indicated a decline in feed frequency for chicks approaching fledging. The average age of the 13 chicks weighed on the night of 31st August 1984 was 61.8 days (S.D. 4.86). Table 5.6 shows the proportions of chicks fed by one or both parents or not at all on each occasion.

Table 5.6 Analysis of variations in feeding frequency during late July and August 1984

For explanation of symbols see text and Table 5.5

Date	n_i	No. Feeds 0	1	2	p_i	θ_i	Z		moon
20-21/7	16	3	5	0	0.313	34.02	-2.608	*	Full
23-24/7	12	1	3	2	0.583	49.78	-0.353		F-L
28-29/7	28	1	7	6	0.679	55.49	+0.515		L-N
07-08/8	32	1	8	7	0.688	56.04	+0.660		N-Ft
10-11/8	32	4	6	6	0.563	48.62	-0.806		Ft
14-15/8	28	5	3	6	0.536	47.06	-1.041		Ft-F
19-20/8	30	1	5	9	0.767	61.14	+1.613		F-L
21-22/8	32	1	7	8	0.719	57.99	+1.044		F-L
23-24/8	30	0	7	8	0.767	61.14	+1.613		L
24-25/8	32	0	9	7	0.719	57.99	+1.044		L
27-28/8	28	4	6	4	0.500	45.00	-1.422		L-N
28-29/8	28	2	8	4	0.571	49.08	-0.668		L-N
31/8-1/9	26	1	8	4	0.615	51.65	-0.187		N

$\bar{n}i = 27.23$ $\bar{\theta}i = 51.92$ $\bar{Z} = -0.046$

Var = 57.412, S.D. = 1.266

With a mean ni of 27.23, the expected variance in θi is 820.7/27.23 = 30.139.
The ratio of the observed variance (57.412) to the expected is not significant ($F = 1.905$, $p > 0.05$).

Notes:-
moon:- F=full; L=last ¼; N=new; Ft=first ¼
dashes indicate phase between two of the above

In this instance the observed distribution of Z was fairly close to the predicted binomial, indicating that there was little variation in feeding frequency with respect to date. This is also confirmed by comparison of the observed variance of θ_i with that predicted. It is worth noting however, that the single instance in which observed feeding frequency differed significantly from the overall average, indicated a reduced feeding probability at full moon. This effect has been noted in previous studies (Harris, 1966b) and is presumably due to the increased risk of predation on light nights causing adults to reduce their activity at the colony. It may be that predation risk to adults is a determinant of feeding frequency during seasons or parts of seasons when food supplies are abundant.

Food conversion efficiency

The regression of net 24 hour weight gain on 4 hour weight increase overnight in 1984 is shown in Fig. 5.5. This regression is highly significant ($p < 0.0001$, $r = 0.847$), and provides useful information on the feed size requirments of Manx shearwater chicks. Chicks which were not fed on a given night lost between 5g and 58g in 24 hours with a regression prediction of 31.2g (S.E. 13.66). The regression line also predicts that in order to maintain or gain weight a chick required an average 4 hour mass increment of at least 54.3g equivalent to a feed size of 69.3g. This is close to the observed mean feed size (Table 5.3). The slope of the line implies a conversion efficiency of 0.58g/g.

The variation in the same regression with age of chick is shown in Table 5.7. The regression was significant at the 1.0% level for chicks aged 16-25 days and at the 0.1% level for all other age classes. These results indicate a decline in food conversion efficiency with chick age. Food requirements were apparently highest among chicks of 36-55 days old, and the results in Table 5.3 suggest that larger feeds were provided for chicks of this age in 1984.

Fig. 5·5 RELATIONSHIP BETWEEN NET 24hr WEIGHT CHANGE AND SUM OF OVERNIGHT 4hr POSITIVE MASS INCREMENTS.

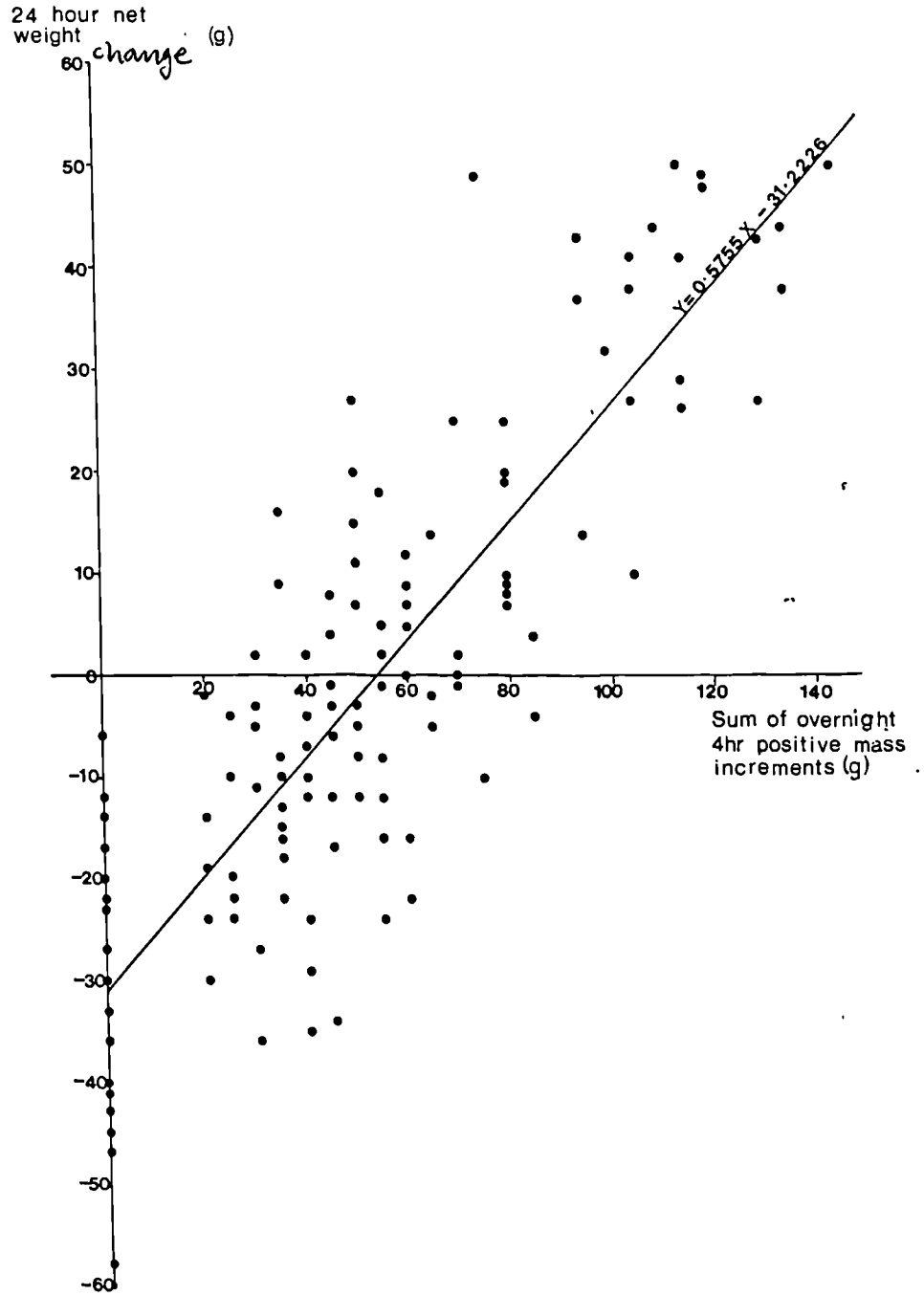


Table 5.7 Characteristics of the regression of 24 hour weight increase on 4 hour night time weight increment for different age classes of chicks in 1984.

Age class	n	Slope (conversion efficiency)	Minimum feed for net 24h weight gain	Net 24 hour weight loss if chick not fed
16-25 days	5	0.81g/g	56.3g	45.9g
26-35 days	13	0.72g/g	43.7g	31.4g
36-45 days	30	0.69g/g	58.6g	40.6g
46-55 days	51	0.55g/g	61.3g	34.0g
56-65 days	52	0.54g/g	47.2g	25.5g

Factors influencing growth rates

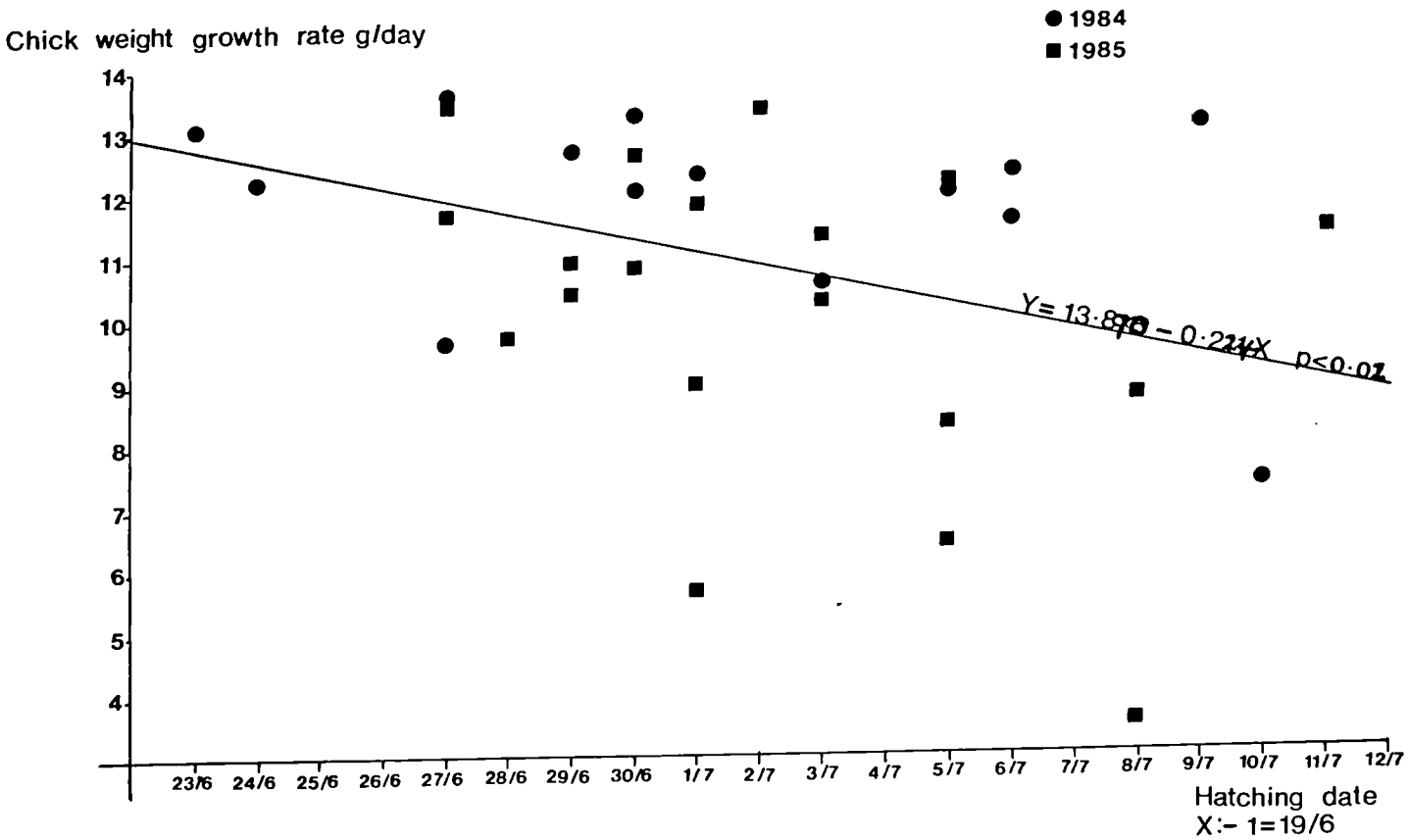
As discussed in Chapter 4, earlier hatched chicks fledge at heavier weights than later ones. This is generally assumed to arise from a deterioration in food supplies and/or feeding conditions later in the breeding season. This hypothesis is lent some support by the relationship between weight growth rate and hatching date shown in Fig. 5.6. It is apparent that later hatching chicks tend to have slower weight growth rates than earlier chicks, with 17% of the variation in growth rate attributable to timing of breeding. This relationship was significant within each year (1984, n = 16, r = -0.442, p < 0.05; 1985, n = 20, r = -0.377, p = 0.05) as well as over both years as shown in Fig. 5.6 (n = 29, r = -0.404, p < 0.01). A similar result has been documented for other seabirds including common guillemots (Hedgren, 1979), Cassin's auklet (Manuwal, 1979) and Brunnich's guillemots (Birkhead and Nettleship, 1982). In cases where a chick fledged from a burrow in both years data from one year were randomly excluded from the combined data set.

Discussion

Diet and food conversion efficiency

Manx shearwaters breeding on Rhum exploit several fish and squid species and apparently seasonally change their diet, presumably according to breeding requirements and food availability (cf. Chp. 4). The ability to exploit a variety

Fig. 5·6 CHICK GROWTH RATE IN RELATION TO HATCHING DATE



of food types in an opportunistic manner has been similarly recorded by Brown et al. (1981) for great and sooty shearwaters wintering along the eastern seaboard of North America.

The results presented in this thesis suggest that the birds exploit more fish when feeding young than earlier in the season when they need only meet their own energy requirements. Squid are clearly not entirely absent from the chicks' diet, as beaks were found in all the chicks and fledglings sampled. Squid have relatively low calorific values by comparison with fish (Pennycuick et al., 1984) and oily fish such as sprats or herring are particularly energy rich (Harris and Hislop, 1978). While none of the 11 proventricular contents samples examined which contained only squid remains were at all oily, 63% of 35 samples containing fish remains were associated with oily liquid. Sprats have a higher energy content than sandeels (Harris and Hislop, 1978) and are therefore of particular value in feeding seabird chicks. The shearwaters may feed extensively at night prior to the chick rearing period as is suggested by their use of squid which are either bioluminescent or which migrate to the surface at night. The necessity to come ashore during the short nights when feeding chicks may be an additional factor influencing their exploitation of fish shoals by day at this time. The grey-faced petrel is a winter breeder in New Zealand and feeds its chicks on a mixed diet of squid, fish and some crustacea. Over 90% of its prey species are bioluminescent and migrate to the surface at night. Night feeding is apparently one aspect of the ecology of this species which enables it to breed in winter when daylength is short (Imber, 1973 & 1976). Audubon's shearwater breeding on the Galapagos feeds its chicks on a mixture of mainly larval fish and crustacea which swarm inshore (Harris, 1969). The use of plankton by this species is energetically feasible due to its small size and the proximity of the prey to the breeding site.

The nature of the food supplied to chicks is clearly of importance in determining growth rates and the rate of provisioning required to sustain growth. Fledging weights of puffins on St. Kilda were reduced in years when the proportion of sprats in the diet declined relative to whiting, since the latter has a lower calorific value (Harris and Hislop, 1978). The slopes and intercepts of net 24 hour mass increments versus the sum of positive 4 hourly mass increments overnight for several species are shown in Table 5.8. These data are taken from Ricklefs (1984), Ricklefs et al. (1985) and from this study.

Table 5.8 Characteristics of the net 24 hour weight gain versus overnight 4 hour mass increment regression for a variety of procellariiforms Figures in slope column are ± S.E.. Number of chick-nights used to calculate each regression are shown in parenthesis.

Species	Slope (food conversion efficiency	Intercept (feed size needed to maintain initial weight.
Leach's storm petrel	0.92 ± 0.04 (71)	15% of adult mass
Phoenix petrel	0.77 ± 0.114 (17)	17% " " "
Manx shearwater	0.58 ± 0.029 (156)	13% " " "
Christmas shearwater	0.42 ± 0.073 (30)	14% " " "
South Georgia diving petrel	0.35 - (9)	35% " " "

Food conversion efficiency presumably reflects, in part, the calorific composition of the food and its similarity in terms of protein content to the composition of chick tissues. The conversion of food to oil in the stomach of adult Leach's petrels prior to regurgitation to the chick is consistent with the very high conversion efficiency noted above which is significantly greater than that of either the

Manx shearwater ($t = 6.699$, d.f. = 225, $p < 0.001$) or the Christmas shearwater ($t = 6.439$, d.f. = 99, $p < 0.001$). Of the two shearwater species given, the *Manx* has a significantly higher conversion efficiency than the Christmas shearwater ($t = 2.179$, d.f. = 184, $p < 0.05$). This may be due to the apparent predominance of fish in the chick diet of the former. By contrast, Christmas shearwater chicks receive a diet containing approximately equal volumes of fish and squid (Harrison et al., 1983).

The inverse relationship between conversion efficiency and maintenance feed size suggested by comparison among Leach's petrel, Phoenix petrel and South Georgia diving petrel is to be intuitively expected. However, the two shearwaters do not fit this pattern as they exhibit both relatively low conversion efficiencies and low maintenance feed requirements. This could arise from differences in B.M.R. between the species considered. Beck (1986) has shown that high B.M.R. is essential to the survival of Antarctic petrels nesting in extremely cold conditions on the Antarctic mainland. It seems likely that the maintenance of homeothermy will place varying energetic demands upon chicks of different species according to breeding site location and so influence the relationship between dietary intake and energy expenditure. The data shown in Table 5.7 also indicate that food conversion efficiency alters as chicks develop, so that care must be taken in comparing this parameter among species.

Chick growth rates

The average weight growth curves recorded for a sample of chicks on Rhum match those found on Skokholm as illustrated in Fig. 5.1. Feeding intervals and probabilities are also similar. Harris (1966b) estimated average feeding interval on Skokholm to be 1.29 days on the basis of daily weighings of two chicks to 0.1g, while twice hourly checks of nine burrows over three nights indicated the probability of

individual parents feeding chicks to be 0.630. If minimal time were spent in actually feeding, the 1.3 day chick feeding interval found at both colonies would enable birds to spend up to 15 hours flying to their feeding grounds. At a flight speed of $14.5ms^{-1}$ (cf. page 59), this would equate to a maximum foraging range of 780km. In reality, it is unlikely that adult shearwaters do travel such large distances to find food for their young. Manx shearwaters at both Skokholm and Rhum are observed to form large flocks just offshore in late afternoon, several hours before coming ashore after dark (Lockley, 1942; pers. obs.), and it seems likely that much of the time at sea is spent on the surface and not in flight. The highly productive waters of the Minches (Bourne and Harris, 1979), ca 100km from Rhum, are clearly within easy reach of foraging shearwaters.

On Rhum, the difference in average growth rates in 1984 and 1985 apparently reflected a lower feeding frequency in 1985 rather than any reduction in the size of meals delivered by individual parents. This may have reflected some difference in food availability between the two years, but most pairs appeared to have no major difficulty in fledging their young. The small shearwater colony on the neighbouring island of Canna has been monitored since 1973 and severe difficulties in rearing chicks have been recorded in only one season. In that year, 1981, fledging success was reduced to 0.25 chicks per egg, and dead chicks that had apparently starved were found in many burrows (Swann and Ramsey, 1982).

A comparison of the weight and wing growth curves of one of the chicks in 1985 which endured long periods of parental neglect, illustrates the developmental priority given to completion of flight feather growth. Harris (1966b) reported a similar result from a twinning experiment conducted on Skokholm. The nine pairs of twins showed much reduced peak and fledging weights as compared with single controls but wing growth was generally not retarded. The

fledging success of the experimental twins was about 0.3 young per nest as compared to the normal 0.95 for single chicks.

The seasonal reduction in individual chicks' growth rates in relation to the timing of hatching, together with the fall in feeding frequency in older chicks, indicate that food availability declines seasonally. This feature of the environment makes it selectively advantageous for pairs to breed as early as possible, as has been discussed in Chapter 4.

Desertion period

Many procellariiform species reportedly desert their chicks prior to fledging, leaving the young to complete growth on their fat reserves. Some examples from the literature are shown in Table 5.9. The Manx shearwater has been generally reported as having a variable desertion period averaging around 8-10 days and ranging up to 18 days (Harris, 1966b; Ralphs, 1955). However, as in the case of many other species in which a desertion period has been reported, the assumption of parental desertion has been largely based on the observed decline in mass from peak weight to fledging. As Burger (1980) has pointed out, this does not necessarily imply that chicks are no longer fed in this period, for the reasons discussed below :-

(1) Some species in which parental feeding is known to continue right up to fledging also exhibit weight loss prior to fledging eg. the Atlantic puffin (Harris 1976). Harris discovered that hand reared puffin chicks voluntarily reduced their food intake prior to fledging when provided with food ad lib.

(2) Ricklefs (1984) has shown that in slow growing altricial seabirds, including procellariiforms, the chicks' greatest energy demands occur at the end of the fledging period when growth is completed and maintenance metabolic

Table 5.9 Desertion periods in procellariiforms.

Species	Breeding site	Migrant	Desertion period	Source
Short-tailed shearwater	Tasmania	Yes	ca. 14 days	Marshall & Serventy (1956)
Great shearwater	Nightingale Is.	Yes	ca. 14 days	Rowan (1952)
Sooty shearwater	New Zealand	Yes	6 - 28 days	Richdale (1963)
Manx shearwater	Skokholm	Yes	2 - 15 days 3 - 18 days	Harris (1966) Ralphs (1955)
Audubon's shearwater	Galapagos	No	None	Snow (1965), Harris (1969)
Fork-tailed storm petrel	Alaska	No	None	Boersma et al., (1980); Simons, (1981)
Grey-faced petrel	New Zealand	No	None	Imber (1976)
Royal albatross	New Zealand	No	None	Richdale (1954)

requirements approach adult values. Thus the food requirements of the chicks are maximal at that part of the breeding season when food availability to the parents apparently declines.

(3) It has generally been assumed that loss of mass over 24 hours from one day to the next implies that a chick was not fed on the previous night. However, as the relationship between net 24 hour mass increment and meal size described in Fig. 5.5 illustrates, this is not necessarily the case and such an assumption will tend to overestimate any desertion period. For example in this study, assumption of net 24 hour weight loss as indicative of lack of feeding would lead to an estimate of average desertion period in 1984 of 5.9 days (S.E. 1.044, n = 15). By comparison, the assumption that only net 24 hour mass deficits exceeding 25g represent absence of feeding in the previous night (cf. Table 5.7), gives a mean of 3.5 days (S.E. 0.376, n = 15) for desertion period. These figures are maxima because it proved impossible to check chicks daily prior to fledging. Chicks have therefore been assumed to have gone without food on the nights for which no data were available.

On the basis of the above, I do not believe there to be a true desertion period for Manx shearwaters on Rhum. However, as shown in Table 5.5, it does appear that chicks are generally fed less frequently over the last 10 days or so prior to fledging. The examples given in Table 5.9 lend support to Warham's (1964) suggestion of variation in this respect among procellariiforms being linked with migratory patterns. Short-tailed and great shearwaters, which are both transequatorial migrants, have highly synchronised and unvarying breeding dates and do appear to have genuine desertion periods with all the adults leaving the breeding grounds to migrate at the same time each year. In these two species, the timing of events in the breeding season is apparently under rigid endocrine control with daylength acting as the proximate factor. Food supplies around the

breeding sites at the start of the breeding season appear abundant and not limiting to egg formation or successful incubation (Marshall & Serventy, 1956; Rowan, 1952). Another migratory species breeding in the Southern hemisphere and migrating North outside the breeding season is the sooty shearwater which also shows a tendency for the adults to depart over a relatively short period. However, the greater spread in laying dates in this species leads to a greater range in the desertion periods experienced by individual chicks (Richdale, 1963).

I have suggested (Chp. 4) that the Manx shearwater, which has a wider latitudinal breeding range than its congeners described above, is less rigidly constrained in its breeding cycle by internal endocrine rhythms synchronised by daylength, but rather responds more immediately to feeding conditions around the breeding colony. Thus, there is considerable variation among individuals in timing of breeding, and chick feeding patterns are modified by the extant environmental conditions rather than being rigidly pre-determined. Further along this continuum of desertion behaviour lie many non-migratory procellariiforms in which adults and newly fledged young continue to feed in the vicinity of the breeding site outside the breeding season. In these species there is no desertion period and adults may continue to visit the nest site even after chick departure. This behaviour presumably occurs as feeding conditions in the area remain sufficient to support both adults and young so that there is no selective advantage to adults in deserting their young.

Chapter 6

PREDATION AND POPULATION DYNAMICS

Introduction

In Section A, I discuss the relationship between brown rats and Manx shearwaters on Rhum. In section B, I attempt to quantify avian predation of Manx shearwaters on Rhum. As Manx shearwaters form an important part of the diet of golden eagles on Rhum, the effect of this unique diet upon the breeding success of golden eagles on the island is also discussed. In the final section, I present a simple model of the population dynamics of the Rhum shearwater population.

A) Rat predation

Introduction

The three species of rat in the genus Rattus, namely the brown rat, R. norvegicus; the black or ship rat, R. rattus; and the kiore or polynesian rat, R. exulans, have all been cited as responsible for changes in the avifaunas of islands which they have colonised through Man's agency. The vast literature on predation of birds by these rats and their impact upon island avifaunas has been reviewed recently and excellently by Atkinson (1985), and I shall not attempt to repeat such a comprehensive survey here.

In assessing the impact of a predator upon a given species of prey, it must be remembered that this depends not upon the actual rate of predation per se, but upon whether or not such predation consistently causes the prey's annual mortality to exceed recruitment (Moors and Atkinson, 1984). It is for this reason that seabirds are particularly vulnerable to predation by introduced mammalian species which

can invade nest sites, such as burrows, inaccessible to resident, mainly avian, predators (Jones and Byrd, 1979). Seabirds are generally strongly K-selected species with low annual productivity and slow recruitment, so that relatively low levels of predation may be sufficient to cause a colony's decline. Burrow-nesting species are especially vulnerable to predators such as rats and Mustelidae which can enter their nests.

Review of literature, combined with direct observations and study of the impact of Rattus spp. on island birds in New Zealand, enabled Atkinson (1985) and Imber (1975, 1978) to identify parameters which appear to be crucial in determining the impact of an introduced species of rat upon a burrow-nesting seabird. These may be summarised as:-

(1) The relative sizes of the rat and bird. Imber (1975) concluded that a petrel colony invaded by rats is at risk if the maximum body mass of the rat is greater than or equal to the mean body mass of the petrel.

(2) The density of the rat population in relation to that of the seabird. This may be determined by several factors including:-

(a) Habitat

(b) The food supply available to the rats in the season when the seabird is absent.

(c) The presence or absence of predators upon the rats themselves

(3) The availability of other foods to the rat population during the seabird's breeding season.

(4) The bird's behaviour, in particular:-

(a) The degree of aggression which it exhibits towards predators.

(b) Constancy of incubation and length of time for which newly hatched young are brooded.

(5) The combined incubation and fledging periods of the seabird and the degree of synchrony of breeding as these factors determine the period of vulnerability to predation.

(6) The timing of breeding in relation to seasonal fluctuations in rat numbers.

Consideration of these factors would suggest that the Manx shearwater population on Rhum is potentially at risk from the free-living population of brown rats on the island. R. norvegicus is the largest of the three Rattus species, with adults weighing up to 600g in Britain (Corbet and Southern, 1977) compared with a mean adult shearwater weight of 400 - 430g (c.f. page 14). The Manx shearwater has a long breeding season with eggs or chicks present in the colony over a 5 month period. Eggs are commonly deserted for periods of several days between incubation shift changeovers, and chicks are brooded for only a few days immediately after hatching. Free-living brown rats in temperate climates breed mainly in summer and autumn (Corbet and Southern, 1977; Bettesworth, 1972) so that the rat population on Rhum will increase over the shearwaters' nesting period each year from a spring low. In theory it would therefore appear that a population of R. norvegicus could severely affect a Manx shearwater population and indeed the Calf of Man colony was apparently destroyed within the space of a few years around 1800 by brown rats from a shipwreck. That colony was re-established following rat control measures (Cramp, Bourne and Saunders, 1974).

It was in view of this potential for the destruction of a Manx shearwater colony by brown rats that the Nature Conservancy Council wanted the relationship between rats and shearwaters on Rhum to be investigated. Casual observations of the colony over the years have not indicated any dramatic decline in the shearwater population, nor have there been any recorded instances of rat predation. However, in view of the large size and conservation significance of the colony and of reported declines in the smaller colonies on neighbouring

Eigg and Canna, which have been suggested as being attributable to rats (Evans and Flower, 1967), there was a need for a more systematic investigation of the rat-shearwater situation on Rhum.

I can find no historical record of the date of arrival of R. norvegicus on Rhum, but the species is thought to have arrived in Britain around 1730 and to have spread slowly with some "remote areas" in Scotland being colonised as late as the mid 19th century (Corbet and Southern, 1977). It is not known whether R. rattus, which R. norvegicus displaced over most of its range (Corbet and Southern, 1977), was ever present on Rhum. It would appear from estate records held in Kinloch castle on Rhum, that large numbers of brown rats have been present on Rhum for at least 100 years and possibly for considerably longer. Any dramatic initial impact of this new predator would therefore be long past and present day effects would be expected to be less obvious and therefore more difficult to detect.

Methods

The following methods were used to monitor fluctuations in numbers of rats within the shearwater colony and to assess the level of predation upon the shearwaters and their eggs/young.

(1) Monitoring of the occurrence of rat tracks and droppings within the main study area on Hallival. In the frequent checks of observation burrows on Hallival, several set routes were regularly followed, and the presence or absence of any rat droppings or other signs of rat activity in these transects was recorded.

(2) As described in Chapter 3, up to 100 observation burrows were regularly checked to obtain data on timing of breeding and breeding success. These checks also enabled the extent of predation of eggs or chicks in these burrows to be assessed. In addition, eggs abandoned by shearwaters in the study burrows in 1984 and 1985 were regularly checked to

discover if such eggs were scavenged by rats. In order to assess the extent of rat activity in the colony over the winter months, 20 hens' eggs were placed in observation burrows at the end of the 1985 breeding season and checked on a visit in mid winter. These were replenished during that visit and checked again on return to Rhum in the spring of 1986.

(3) Twelve Blederberry cage traps, spaced at ca. 20m intervals along a straight line transect on the N.E. face of Hallival, were kept prebaited over the following periods:

1984:- 4th July - 5th October

1985:- 14th March - 7th October

1986:- 24th April - 6th June

and 7th June - 1st September (6 traps only)

The bait used was "sausage rusk" which is used commercially by butchers as a filler. All traps were sited alongside rock edges and had stone walls and roofs built around them to provide cover. The presence of rat droppings in and around these traps was monitored and in addition the traps were periodically set overnight to catch any visiting rats. The 6 traps removed from Hallival on 6th June 1986 were used until 3rd July in a similar fashion in woodland adjacent to the shore on the south side of Loch Scresort, approximately 1km from Kinloch. This was as a control to ascertain dropping deposition and rat capture rates in an area where there was abundant evidence of rat activity.

(4) Altogether, 180 droppings were collected from several sites on Rhum in 1984 and 1985. The droppings collected at each site on a given date were examined as a unit under a low power binocular microscope after being broken up in water. Following Drummond (1960) the quantities of each component were roughly estimated as little (1-5%), moderate (6-50%), predominantly (51-99%) or entirely (100%). In addition, the entire stomach contents of two rats, one which died in a trap on Hallival on 29-30th September 1984 and the other killed by a domestic cat in Kinloch on 19th June 1984, were examined.

(5) In 1984, soap and paraffin wax baits were placed under rock edges at 26 sites along two randomly selected transects on the N.E. face of Hallival. These were replaced as necessary between 28th May and 4th October. It was hoped that an index of rat activity on Hallival would be provided by the extent to which these items were gnawed upon by rats over the course of the summer. However, this method was not successful as the baits were repeatedly removed by hooded crows or eaten by field mice.

Results

There was no predation of viable eggs or chicks in the observation burrows in 1984, 1985 or 1986.

The monthly occurrences of rat droppings and other evidence of rat activity along the routinely followed observation transects on Hallival is shown in Table 6.1.

Table 6.1 Rat signs seen along observation burrow transects March to October 1984, 1985 and 1986.

Month	No. of days covered			No. of days on which rat signs found: Droppings			Snow tracks			Rat seen		
	'84	'85	'86	'84	'85	'86	'84	'85	'86	'84	'85	'86
March	9	8	0	0	1	-	1	0	-	0	0	-
April	16	14	1	4	5	1	0	0	0	1	0	0
May	20	18	7	0	1	0	-	-	-	0	0	0
June	12	18	11	0	0	0	-	-	-	0	0	0
July	17	12	9	1	0	0	-	-	-	0	0	0
August	19	13	6	0	0	0	-	-	-	0	0	0
Sept.	14	10	0	1	1	-	-	-	-	0	0	-
October	2	4	0	0	2	-	-	-	-	0	0	-
Dec/Jan	0	4	0	-	1	-	-	1	-	-	1	-

These results indicate that rat activity in the study area was minimal from June to August with droppings being found on only 1 of 117 visits. Activity increased in September and October with droppings found on 4 of 30 visits. The limited data from mid-winter of 1985/86 indicate that

relatively large numbers of rats were still present at that time with evidence of activity being found on 3 out of 4 visits. In March and April evidence of activity was found on 28% of visits but by May this had fallen to 2.2%. The Chi^2 analysis shown in Table 6.2 indicates that the seasonal differences in the occurrence of droppings are significant at the 0.1% level.

Table 6.2. Chi^2 analysis of seasonal differences in the occurrence of rat droppings in the study area. Data for all years combined.

a) Comparison of spring, summer and autumn

	March/April	May to Aug.	Sept/Oct	Total
Droppings found	O = 11 E = 3.4	O = 2 E = 11.5	O = 4 E = 2.1	17
Droppings not found	O = 37 E = 44.6	O = 160 E = 150.5	O = 26 E = 27.9	223
Total	48	162	30	240

$\chi^2 = 28.59$, d.f. = 2, $p < 0.001$

As some of the expected frequencies in Table 6.8a are below 5, the spring and autumn observations were combined for comparison with summer as shown in Table 6.8b.

b) Comparison of summer with spring and autumn combined

	March/April Sept/Oct	May to August	Total
Droppings found	O = 15 E = 5.5	O = 2 E = 11.5	17
Droppings not found	O = 63 E = 72.5	O = 160 E = 150.5	223
Total	78	162	240

$\chi^2 = 26.10$, d.f. = 1, $p < 0.001$

The fates of abandoned shearwater eggs in the observation burrows in 1984 and 1985 are given in Table 6.3. The average period between desertion and consumption of the 12 eggs eaten by rats in 1984 was 70 days (S.D. 29.78, range 24-106 days). Two of the eggs were taken in the last week of

June, one in July, one in August, seven in September and one in October. These results show that some rats were present in the study area between June and August. However, as was suggested by the observations in Tables 6.1 and 6.2, there was a marked increase in the level of rat activity in September with 58% of the eggs being taken in that month.

Table 6.3 Fate of shearwater eggs abandoned in the observation burrows in 1984 and 1985 from time of desertion until the end of the field season on 5th and 7th October respectively.

	1984		1985	
	No.	%	No.	%
Eggs abandoned	52		16	
Broken by author	2	3.8	0	0.0
Broken by shearwaters	3	5.8	2	12.5
Buried by shearwaters	24	46.2	1	6.2
Kicked out of burrows	1	1.9	0	0.0
Eaten by invertebrates	1	1.9	1	6.2
Remained intact	1	1.9	1†	6.2
Eaten by rats	12*	23.1	3**	18.8
Disappeared- possibly buried, kicked out or taken away by rats	8	15.4	8	50.0

Notes:- * 6 of these eggs had been buried by shearwaters and subsequently unearthed by the author.
** 1 of these eggs had been buried by shearwaters and subsequently unearthed by the author.
† this egg disappeared between 7/10 and 25/12/85.

The fates of the hens' eggs placed in observation burrows in the winter of 1985/86 are given in Table 6.4. Of the 20 hens' eggs initially placed in shearwater burrows, 11 were put in a group of 11 adjacent observation burrows, while the remaining 9 were placed singly in scattered burrows. This was done to try to determine whether rats search randomly or systematically for abandoned eggs. As shown in Table 6.5, there was no indication that grouped eggs were removed more readily than scattered eggs which suggests a random search behaviour. The results indicate a peak in scavenging behaviour in mid-winter. In late September and

early October eggs were removed at an average rate of 0.20 per day. Between 7th October and 25th December all of the 16 available eggs were taken so that a true depletion rate cannot be calculated. However, in the 9 day period over which checks were made in mid-winter, the removal rate was 0.55 eggs per day. Between early January and late April only 3 of 21 eggs were taken equivalent to 0.03 eggs per day.

Table 6.4 Fates of hens' eggs placed in observation burrows over the winter of 1985/1986.

	Interval and Egg Position							
	17/9/85-7/10/85		7/10/85-25/12/85		25/12/85-3/1/86		3/1/86-24/4/86	
	N	S	N	S	N	S	N	S
No. of eggs at start of interval.	11	9	11	5	12	11	11	10
No. broken by author in interval.	0	1	0	0	0	0	0	0
No. intact at end of interval.	11	5	0	0	9	9	10	8
No. eaten by rats by end of interval.	0	1	6	5	2	1	1	1
No. vanished by end of interval (presumed taken by rats).	0	2	5	0	1	1	0	1

Key to letters denoting eggs' positions:-
N:- single eggs placed in neighbouring burrows
S:- single eggs placed in scattered burrows

Table 6.5 Chi^2 analysis of egg removal from neighbouring versus scattered burrows.

	Neighbouring burrows	Scattered burrows	Total
Egg taken	O = 15 E = 15	O = 12 E = 12	27
Egg not taken	O = 10 E = 10	O = 8 E = 8	18
Total	25	20	45

$\chi^2 = 0$, d.f. = 1, p = 1

The frequency and timing of the occurrence of rat droppings in the prebaited cage traps is shown in Table 6.6. The figures in the droppings column indicate the sum, over the given time interval, of the number of traps in which droppings were found on each check

Table 6.6 Occurrence of rat droppings in prebaited cage traps

Year	Site	No. of traps	Period	No. times checked	Droppings	Interval in which droppings found
1984	Hill	12	4/7 - 5/10	22	4	31/8 - 5/10
1985	Hill	12	1/4 - 7/10	48	17	3/9 - 7/10
1986	Hill	12	24/4 - 6/6	7	3	1/5 - 11/5
1986	Hill	6	7/6 - 1/9	14	0	-
1986	Shore	6	10/6 - 3/7	21	5	13/6 - 3/7

These results again indicate a minimal level of rat activity in the study area in June, July and August with peak activity in September. By contrast, droppings were deposited in the shore traps during June. The maximum rate of dropping deposition in hill traps of 0.04 droppings per trap day in the period 3rd September to 7th October 1985, was equal to that recorded in the shore traps in June 1986.

The numbers of rats captured in the cage traps each month is shown in Table 6.7. The high capture rate of rats in the traps set near the shore in June 1986 indicates that the Rhum brown rats are not trap shy. The very highly significantly lower capture rate within the shearwater colony (χ^2 = 100.2, d.f. = 2, $p < 0.001$) therefore indicates that the population density is much less than on the coast. As with the results already described, the seasonal pattern

of trapping rate in the study area indicates a marked increase in rat activity in September.

Table 6.7 Capture rates of rats in cage traps

	April	May	June	July	Aug.	Sep.	Oct.
Hallival, 1984							
No. trap nights	0	0	0	12	48	12	0
No. rats caught	-	-	-	0	1	3	-
Hallival, 1985							
No. trap nights	24	36	24	48	36	36	24
No. rats caught	0	0	0	1	1	3	1
Hallival, 1986							
No. trap nights	0	0	12	0	0	0	0
No. rats caught	-	-	0	-	-	-	-
Shore, 1986							
No. trap nights	0	0	18	0	0	0	0
No. rats caught	-	-	12	-	-	-	-

The composition of rat droppings collected in 1984 and 1985 is shown in Table 6.8. In addition to the droppings, the stomach contents of two rats were examined. The first died in a cage trap on Hallival in September 1984 and its stomach contents were mainly insect larvae with small amounts of plant material, down, hair, egg and adult insect carapace. The second rat was killed by a cat in Kinloch in June 1984 and was found to have been feeding predominantly on plant material and small numbers of insects.

These results indicate that free-living rats on Rhum ate mainly plant material (plant remains in 97.6% of samples) but also took invertebrates (remains in 75.6% of samples). Vertebrate material was found in 58.6% of samples, but generally in minimal quantities, and was probably mainly obtained through scavenging. The diet indicated is very similar to that described for other free-living Rattus populations eg. R. norvegicus on South Georgia (Pye and Bonner, 1980) and in a salt marsh in Essex (Drummond, 1960); and R. rattus on an island in Tasmania where the rats scavenged in a short-tailed shearwater colony but did not apparently act as predators (Norman, 1970).

Table 6.8a Rat Droppings Contents:-
Shearwater colony, 1984

	Sample number								
	1	2	3	4	5	6	7	8	9
Month	Mar	Mar	Apr	Apr	Apr	Jun	Jul	Jul	Sep
Site	O	O	B	O	O	T	O	B	B
No. droppings	1	1	1	2	1	4	1	5	4
Plant	E	E	E	E	L	M		M	M
Insect:-									
Adult					L	M	P	M	
Larvae								M	M
Down								M	M
Feather					M				
Skin					M				
Bone					M				
Egg								M	L
Soil						L	L		
Bait						M			

Table 6.8b Rat Droppings Contents:-
Outside shearwater colony, 1984

	Sample No.		
	1	2	3
Month	Mar	May	May
Site	Path	Shore	Shore
No. droppings	19	9	2
Plant	P	M	
Insect:-			
Adult	L	M	
Larvae	L		
Amphipoda		M	P
Mollusc		M	L
Feather		L	
Flesh		P	
Bone		L	
Soil	L		

Table 6.8c Rat Droppings Contents:-
Shearwater Colony, 1985

	Sample No.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Month	Mar	Mar	Mar	Apr	Apr	Apr	Apr	Apr	Apr	May	Sep	Sep	Sep	Oct	Dec	Dec	Dec	Dec	Dec
Site	O	O	O	B	B	B	O	O	B	O	B	T	T	B	B	B	O	B	T
No. droppings	2	2	3	10	2	2	7	4	1	1	2	1	1	3	7	1	5	13	6
Plant	M	P	P	M	P	P	P	P	P	P	M	M	M	M	P		P	M	M
Insect:-																			
Adult		L	L	L	L			L	L		M	M	M	M	M		M		
Larvae			L			L	M		L		M	M	M	M					
Mollusc										L									
Down	M			L		L	L			L	M	M	M	L	M		L	M	M
Feather												M	M						L
Skin	M																	L	L
Flesh																M			
Bone	M															M			L
Hair											L					M		L	M
Egg				L								L	L	L	L				L
Soil				P															

Table 6.8d Rat Droppings Contents:-
Outside Shearwater Colony, 1985

	Sample No.							
	1	2	3	4	5	6	7	8
Month	Mar	Mar	Apr	Apr	May	Jun	Jun	Sep
Site	Egle	Strm	Egle	Egle	Hill	Shre	Strm	Vllg
No. droppings	3	3	3	4	3	34	5	2
Plant	P	P	P	P	P	P	M	P
Insect:-								
Adult	L	L			M	L	M	
Larvae							L	
Amphipoda						M		M
Mollusc						L		
Down					L			
Skin						M		
Bone		L				L		
Hair			L		L	L		L
Egg				L	L	L	L	

Key to abbreviations used in Table 6.8:-

a) Description of contents

E = entirely (100%)
P = predominantly (51 - 99%)
M = moderate (6 - 50%)
L = little (1 - 5%)

b) Description of sites

O = dropping on open ground, not next burrow or trap
B = dropping in or near burrow entrance
T = dropping in or near cage trap
Shre = dropping on shore
Egle = dropping found at golden eagle roost
Strm = dropping found on stream or river bank
Vllg = dropping found in Kinloch

Discussion.

The results presented above lead to several conclusions about the activity of rats within the Rhum shearwater colony:-

(1) Brown rats on Rhum are not active predators of Manx shearwaters, their eggs or young. They do act as scavengers of abandoned eggs and dead birds in the autumn and over all or part of the winter.

(2) The density of rats within the shearwater colony is low at all times as compared to that around the coast. The high capture rate in traps placed near the coast indicates that the low capture rate within the shearwater colony was a genuine indication of rat density and did not arise from Rhum rats being trap-shy.

(3) Minimal numbers of rats were present in the shearwater colony during the birds' breeding season. Increased numbers were present in the autumn, winter and early spring, with peak activity between September and January. Monitoring of general signs of rat activity within the shearwater colony, the seasonal pattern of occurrence of droppings and rate of capture of rats within prebaited traps, and the timing of scavenging of deserted eggs all support this conclusion.

There are two possible explanations for the observed seasonal pattern in rat activity in the study area on Hallival:-

(1) There is a resident rat population within the study area whose numbers fluctuate seasonally due to breeding. Free living populations of brown rats in cool temperate climates have a seasonal peak in breeding during the summer which leads to a maximum population peak in autumn and a minimum in spring (Corbet and Southern, 1977). Rat activity within the shearwater colony does peak in autumn but the rise appears to be more sudden than would be expected if a resident population were breeding throughout the summer, and the population minimum apparently occurs in mid-summer rather than in spring.

(2) There is a migration of rats from the shore to the colony in autumn. Population pressure among the shore-living rats should peak in early autumn due to summer breeding, and is likely to be severe in view of the high densities present in June well before the population peak. The availability of favoured plant foods declines at this time as temperatures fall and primary productivity decreases. Invertebrate activity also declines at the onset of winter. That rats do move at this time, in search of fresh food supplies, is suggested by the annual movement of rats into dwellings in Kinloch during the autumn (personal observation and communication from residents on Rhum). Similarly, a study of rural brown rats in Wisconsin reported in Twigg (1975) found that the rats moved to human habitation and other locally abundant food sources in winter. On Rhum, rats forced to move away from the shore in search of alternative food sources in the winter, and which are unable to gain access to buildings, are faced with wide tracts of unproductive moorland which is not a favoured rat habitat (Twigg, 1975). However, any rats which cross this natural barrier, have access to a rich supply of food in the abandoned eggs and dead chicks in the shearwater colony. Long distance movement of up to 6km in a night has been recorded among brown rats (Twigg 1975).

If rats do immigrate to the shearwater colony in the autumn, and only a tracking study of individual animals could confirm this, the question remains as to why these rats apparently do not remain throughout the year. There are several possible explanations:-

(1) Food shortage in late winter/early spring forces the rats to leave the colony before the area becomes productive of fresh plant and invertebrate food in summer.

(2) The shortening nights in spring and summer do not allow the rats sufficient predator-free foraging time to meet their energy requirements. Brown rats are mainly nocturnal with peak activity at dusk and the hours just before dawn

(Corbet and Southern, 1977). The intensively grazed short vegetation on Hallival would provide little cover from avian predators for small mammals forced to forage by day.

(3) The returning shearwaters drive the rats from the shearwater burrows which the rats inhabit during the winter.

Of these possibilities the last seems unlikely as there are always unused burrows present in the colony although these are visited by prospecting shearwaters (pers. obs.). There are also extensive boulderfields throughout the colony which could provide suitable cover for rats. Furthermore, it is not certain that a shearwater could evict a rat from a burrow, as adult shearwaters confused by house lights in Kinloch have been observed to be preyed upon by rats (F. Guiness, pers. comm.). Predation might play a part in controlling rat numbers in the colony as golden eagles on Rhum do feed on rats (c.f. Section B). However, the results of the hens' eggs provision experiment suggest that rat activity declines most dramatically in late winter, and this is consistent with the hypothesis that food shortage reduces the population at this time. Further evidence for this comes from the observations of Swann and Ramsey (1982) on Canna. The shearwater population there nests on grassy cliffs adjacent to the shore. In most of the 13 years over which this colony has been studied, there has been no evidence of rat predation on shearwaters or their eggs and chicks. The major exception to this occurred in 1982 when breeding success in the colony was reduced by rat predation of eggs and chicks to 0.02 chicks fledged per egg laid. In the previous summer there had been high mortality of shearwater chicks and adults late in the breeding season apparently due to food shortage. Swann (pers. comm.) suggests that this superabundant supply of winter food within the shearwater colony enabled scavenging rats to overwinter in the colony and remain as predators in the 1982 season. A poisoning campaign was successful in preventing predation in the following season.

Unfortunately, the Rhum colony was not under observation between 1974 and 1983, so it is unknown if similar events occurred in 1981 and 1982. However, the situation of the Rhum colony as a habitat "island" buffered from the coast by unproductive moorland, may serve to protect it from such events, as it is unlikely that large numbers of rats would ever migrate to it. In the event of a larger than normal population managing to overwinter in a year of exceptional abundance of abandoned eggs or dead chicks, these animals and their offspring would then be subject to golden eagle predation in spring and summer and to food shortage in the following winter.

In conclusion, the current situation on Rhum appears to be that brown rats do not act as predators of shearwaters but that a small migratory population scavenges shearwater remains in the autumn and winter. Thus, while the Manx shearwater's breeding biology does make it potentially vulnerable to rat predation, the existing colony's location and habitat prevents a rat population from becoming established within the birds' breeding grounds. Similarly, Campbell (1968) found that R. rattus predation of ancient murrelet eggs on an island in British Columbia was restricted to upper beach areas and did not occur on cliffs or forest slopes. There is some circumstantial evidence to suggest that in the past rats may have been active predators of shearwaters on Rhum and caused a contraction of the birds' breeding grounds. In 1871, Gray referred to the shearwater colony as having previously extended to the coast, and it is possible that following the arrival of rats these lower shearwaters were preyed upon until the current situation of an inland "island" colony was attained. Similarly, in their survey of the breeding distribution of black guillemots in the Orkney and Shetland islands, Ewins and Tasker (1985) found that low coastal nest sites were less common on islands with rats or stoats than on islands free of these predators.

B) Avian Predators

Introduction

The three resident species of avian predator of Manx shearwaters on Rhum are the golden eagle, great black-backed gull and peregrine falcon. The impact of each of these predators on the shearwater population is considered below. In addition, I examine the implications for Rhum's golden eagle population of exploiting shearwaters and other seabirds as prey.

Golden Eagles

Between 3 and 5 pairs of golden eagles hold territories on Rhum each year (Corkhill, 1980; Love, 1980). In order to assess the numbers of shearwaters eaten per annum, I made regular fortnightly visits to 15 roost sites in two accessible territories between 20th March and 3rd October 1985. All pellets and other prey remains were collected. Pellets were teased apart and the prey remains which they contained, usually bones, hair and feathers, were identified by reference to my own collection of prey species available on Rhum and the comprehensive collection of Scottish fauna held at the Royal Scottish Museum in Edinburgh. The results of this analysis are shown in Table 6.9 together with Corkhill's (1980) observations for the period 1957 to 1976.

The two sets of data are broadly similar and indicate the unusually high percentage of avian prey, and especially seabirds, in the diet of the eagles on Rhum. This reflects the absence of rabbits and hares from Rhum. Elsewhere in Scotland, these species, together with red grouse and ptarmigan, comprise about 90% of the summer diet of golden eagles (Brown and Watson, 1964). The higher percentage of red deer in Corkhill's figures probably arises from his use of all records, including sightings of eagles feeding, in his calculation of relative frequencies. Eagles will often feed on larger prey in situ, especially when they are not feeding young as was the case in both territories in

Table 6.9 Prey of Golden Eagles on Rhum from April to September 1985 (this study) and in the same months from 1957 to 1976 (taken from Corkhill, 1980).

	1985				1957 - 1976	
Prey	Pellet	Other	Min. No.	%	All records	%
Red deer:-	6	0	4	5	17	11
adult	-	-	-	-	6	4
calf	-	-	-	-	11	7
Goat	8	0	5	6	4	3
Brown rat	9	2	7	9	3	2
Field mouse	1	0	1	1	0	0
Rat/mouse	1	0	1	1	0	0
Rabbit	0	0	0	0	2	1
Total mammals	25	2	18	22	26	17
Fulmar	0	1	1	1	40	25
Gull	0	1	1	1	29	19
Shearwater	30	1	29	36	28	18
Shag	0	2	1	1	0	0
Red grouse	17	3	17	21	13	8
Cuckoo	2	0	2	3	0	0
Auk	0	1	1	1	0	0
Kittiwake	0	0	0	0	8	5
Crow	0	0	0	0	4	3
Bird < shw	2	1	3	4	-	-
Bird = shw	3	0	2	2	-	-
Bird > shw	4	0	3	4	-	-
Bird unknown	3	0	3	4	8	5
Total birds	61	10	63	78	130	83
(Seabirds	30	6	33	41	105	67)

Notes on Table 6.9

1) Figures in the "pellet" column indicate the number of pellets which contained the given prey item.

2) "Other" refers to prey remains not in pellet form.

3) "Min. No." is the minimum number of prey represented by all the remains found. This makes allowance for the fact that one prey item may be represented by more than one pellet collected at a given site at one time. For large prey items such as deer, it was assumed that all pellets containing remains of that species which were collected in a single territory on a given date originated from the same animal. For smaller prey such as grouse and shearwaters, the minimum number of prey represented in all the remains collected at one time within a territory was assessed from the total numbers of items such as skulls and claws found.

4) %- for the 1985 data this is the frequency of occurrence of the given prey item on the basis of the minimum number figures, and for Corkhill's figures this is the frequency of occurrence of the given prey for all prey remains and sightings of feeding eagles combined.

5) Where possible, unidentified bird remains collected in 1985 were catageorised by size in relation to a Manx shearwater eg. bird < shw indicates remains of unidentified birds judged to be smaller than shearwaters.

1985. This may reduce the number of pellets from such prey to be found at roost sites. Additionally, several pellets may be produced from a single large prey item so that numbers of such prey may be overestimated by simply totalling pellets.

In order to establish a more meaningful assessment of the relative importance of different prey in the diet, it is necessary to convert the minimum number frequency figures to the biomass of prey which they represent. This is done for my 1985 data in Table 6.10. The weights for the various prey are derived from several sources as indicated, while the wastage factors follow those used by Brown and Watson (1964). The assumed ratio of 3 calves to 1 adult for red deer is based on Corkhill's (1980) findings as I did not assess this directly.

In terms of biomass of prey, it is apparent that large mammals are the most important prey of golden eagles on Rhum during the summer months. Whereas eagles may take small deer calves live, much of this component of the diet will be scavenged from dead animals. This contrasts with the summer diet of golden eagles elsewhere. In the Eastern Highlands of Scotland, Brown and Watson (1964) found carrion to represent only 10% of the total biomass of prey taken in the summer. In North West Sweden, Tjernberg (1981) found birds and mammals to be of equal importance in terms of biomass, with Tetraonidae and mountain hares comprising 74% of total intake. This reliance upon scavenged material may be partly responsible for the generally poor reproductive success of golden eagles on Rhum. Corkhill (1980) recorded an average success rate of 0.37 chicks per breeding attempt, equivalent to 0.29 per occupied territory, over the years 1957 to 1976. The highest breeding success rate yet recorded on Rhum was in 1977 when 5 pairs reared 3 chicks. By comparison, Everett (1971) found an average success rate of 0.58 young per pair over seven areas of Scotland in the period 1964 to 1968, while Brown and Watson (1964) give 0.8 young per pair for the

Table 6.10 The relative importance of different prey items in the diet of golden eagles on Rhum from April to September 1985.

Prey	Live Weight (kg)	Wastage factor (%)	Available weight (kg)	Min. No. found in 1985	Total biomass (kg)	%
Red deer:-						
doe*	51	40	30.6	1	30.6	18
calf*	27	40	16.2	3	48.6	29
total	-	-	-	4	79.2	47
Goat**	25	50	12.5	5	62.5	37
Rat**	0.50	20	0.40	7	2.8	2
Apodemus**	0.02	20	0.01	1	0.0	0
Total mammal	-	-	-	-	144.5	86
Fulmar†	0.80	20	0.64	1	0.64	<1
Gull†	1.00	30	0.70	1	0.70	<1
Shearwater	0.43	20	0.34	29	9.98	6
Shag§	1.75	30	1.23	1	1.23	1
Red grouse*	0.64	20	0.51	17	8.70	5
Cuckoo§	0.10	20	0.08	2	0.16	<<1
Auk†	0.90	20	0.72	1	0.72	<1
Bird<shw	0.20	20	0.16	3	0.48	<<1
Bird=shw	0.40	20	0.32	2	0.64	<1
Bird>shw	0.80	20	0.64	3	1.92	1
Total bird	-	-	-	-	25.2	14

Sources for weights:-

* Brown and Watson (1964)

** Corbet and Southern (1977)

† Bourne and Bogan (1972)

§ Pforr and Limbrunner (1982)

Eastern Scottish Highlands. Recent studies of Scottish golden eagles have shown that whereas territory density is correlated with total food availability (ie. including carrion), breeding success is positively correlated with the availability of live prey early in the breeding season (Dr. J. Watson, pers. comm.). In March and April 1985, red grouse and brown rats were the most frequently occurring prey in the remains examined as shown in Table 6.11. However, in terms of biomass red deer was the most important item representing an estimated 74.4% of the total intake in these months. Manx shearwaters were not found in prey remains until May.

Table 6.11 Prey of Golden Eagles on Rhum in March and April 1985.

Prey	Pellet	Other	Min. No.	%
Red deer	4	0	2	7
Goat	2	0	1	4
Brown rat	7	1	4	15
Field mouse	2	0	1	4
Total mammals	15	1	8	30
Fulmar	0	5	3	11
Gull	0	1	1	3
Shag	0	2	1	4
Red grouse	9	4	10	37
Cuckoo	1	0	1	4
Auk	0	1	1	3
Bird < shw	1	0	1	4
Bird unknown	1	0	1	4
Total birds	12	13	19	70

Once the relative contribution of different prey types to the total dietary intake is known, it is possible to calculate the total numbers of any given prey consumed over a given period of time. Brown and Watson (1964) estimated that an adult eagle requires 230g of food per day. On average, a growing chick was estimated to require the same amount. Brown and Watson (1964) further estimated that non-breeding

adults and independent young represent 20% of the Scottish eagle population. Assuming an average breeding success on Rhum of 0.29 chicks per pair (Corkhill 1980), it is possible to calculate the total food requirement of the Rhum eagle population over one summer as shown below:-

Population composition in March:-

4 breeding pairs

2 non-breeding birds

With a daily food requirement of 230g per bird per day, the total food consumption of the adult population between April and September will be:-

$$10 \times 230 \times (30+31+30+31+31+30) = 420900g \text{ or } 420.9kg$$

Food will also be required for $4 \times 0.29 = 1.16$ chicks over approximately 5 months from hatching in late April/early May giving an additional summer food requirement of:-

$$1.16 \times 230 \times 150 = 40020g \text{ or } 40.0kg$$

The estimated average total required intake for the Rhum golden eagle population between April and September is therefore:-

$$420.9 + 40.0 = 460.9kg$$

From Table 6.10, 6% of this will be provided by shearwaters:-

$$460.9 \times 0.06 = 27.7kg$$

With 0.344kg of food provided by a single shearwater this weight of food represents:-

$$27.7 \div 0.344 = 80 \text{ birds}$$

This order of predation is not sufficient to have any significant impact upon a population of the order of magnitude, 10^5, of the Rhum shearwater colony. However, shearwaters are an important component of the live prey of golden eagles on Rhum and one pair has been observed to feed its chicks almost exclusively on these birds (Wormell, 1965). A pair raising a single chick entirely on shearwaters would require an estimated 100 birds (34.5k ÷ 0.344) which would again not represent any threat to the shearwater population.

Golden Eagle Breeding Success in Relation to Diet

There has been some speculation that high organochlorine levels in seabirds might be responsible for the frequent reproductive failure of the Rhum golden eagles (Corkhill, 1980; Love, 1980). While this subject is outside the main scope of this thesis, in view of its importance to the avian ecology of Rhum, it is discussed briefly below. Data on organochlorine residue and mercury levels in Rhum golden eagle eggs and feathers are compiled in Table 6.12, together with information on concentrations of the same chemicals in Manx shearwaters, fulmars and kittiwakes.

These data illustrate the relatively high levels of organochlorine residues and mercury in Rhum golden eagle eggs and feathers compared with other sites in Scotland. This apparently results from the Rhum eagles' extensive use of seabirds as live prey. High levels of heavy metals and organochlorines accumulate along the marine food chain in which seabirds are top predators (Furness and Monaghan, 1987). The relationship between breeding success and diet among the four regularly occupied territories on Rhum, shown in Fig. 6.1, suggests that the intake of fulmars, and to a lesser extent kittiwakes, affects the likelihood of successful breeding while consumption of shearwaters or scavenged material does not. Of the seabirds exploited by golden eagles on Rhum, shearwaters have relatively low levels of mercury and PCBs in their tissues compared with fulmars and kittiwakes (cf. Table 6.12). It might therefore be inferred that the low breeding success of golden eagles on Rhum results from accumulation of toxins in their tissues. However, as yet it is not clear at what levels PCBs and heavy metals are actually detrimental to golden eagles. The high percentage of scavenged material taken by the Rhum eagles may also be a cause of the Rhum eagles' generally poor reproductive preformance as discussed above. However, the lack of correlation between breeding success and intake of non-live prey within the island, suggests that pollutants

Table 6.12 Organochlorine residues and mercury (ppm, wet weight) in Rhum golden eagles and in seabirds found in the adults' diet.

Material	Source	Year	Ref.	PCB	DDE	Total	Hg
5 eggs	Rhum	1964/5	*	-	-	3.06	-
44 eggs	Scotland	1964/5	*	-	-	1.61	-
Eggs	W. Scot.	'66-71	**	-	0.14	0.23	-
Eggs	E. Scot.	'66-71	**	-	0.03	0.06	-
1 egg	Rhum	1970	**	3.0	2.3	5.7	-
1 egg	Rhum	1971	*	3.0	-	-	-
1 egg	Rhum, site A	1972	**	3.0	1.5	4.7	-
Eggs	W. Scot.	1972-4	**	-	0.15	0.18	-
Eggs	E. Scot.	1972-4	**	-	0.09	0.10	-
1 egg	Rhum, site C	1975	*	0.7	2.69	-	-
1 egg	Rhum, not C	1975	*	0.6	2.32	-	-
1 egg	Rhum, site C	1976	**	6.2	4.1	12.5	1.06
1 egg	Rhum	1978	**	3.4	2.7	6.2	0.77
1 egg	Rhum, site A	1984	**	16.5	2.09	18.66	0.3
1 egg	Rhum, site A	1985	**	13.5	1.73	15.5	0.9
1 egg	Rhum, site D	1985	**	7.5	1.43	9.25	0.7
3 feathers	Rhum, site D	1985	**	-	-	-	8.2
6 feathers	Rhum, site A	1985	**	-	-	-	5.4
10 feathers	E. Scot.	1985	**	-	-	-	0.9
Shw liver	Rhum	1971	***	0.5	-	-	-
Shw liver	Rhum	1971	***	0.2	-	-	-
Shw liver	Rhum	1984	**	0.15	0.06	-	-
Shw liver	Rhum	1984	**	0.12	0.07	-	-
4 Shw:-	St. Kilda	1977	†				
livers				-	-	-	10.2
feathers				-	-	-	1.15
Fulmar:-	N. Atlantic	1971	***				
10 livers				4.8	-	-	-
5 Fulmar:-	St. Kilda	1977	†				
livers				-	-	-	29.4
feathers				-	-	-	3.34
Kittiwake:-	N. Atlantic	1971	***				
11 livers				4.7	-	-	-
30 feathers	(Scotland)	1986	††	-	-	-	3.0

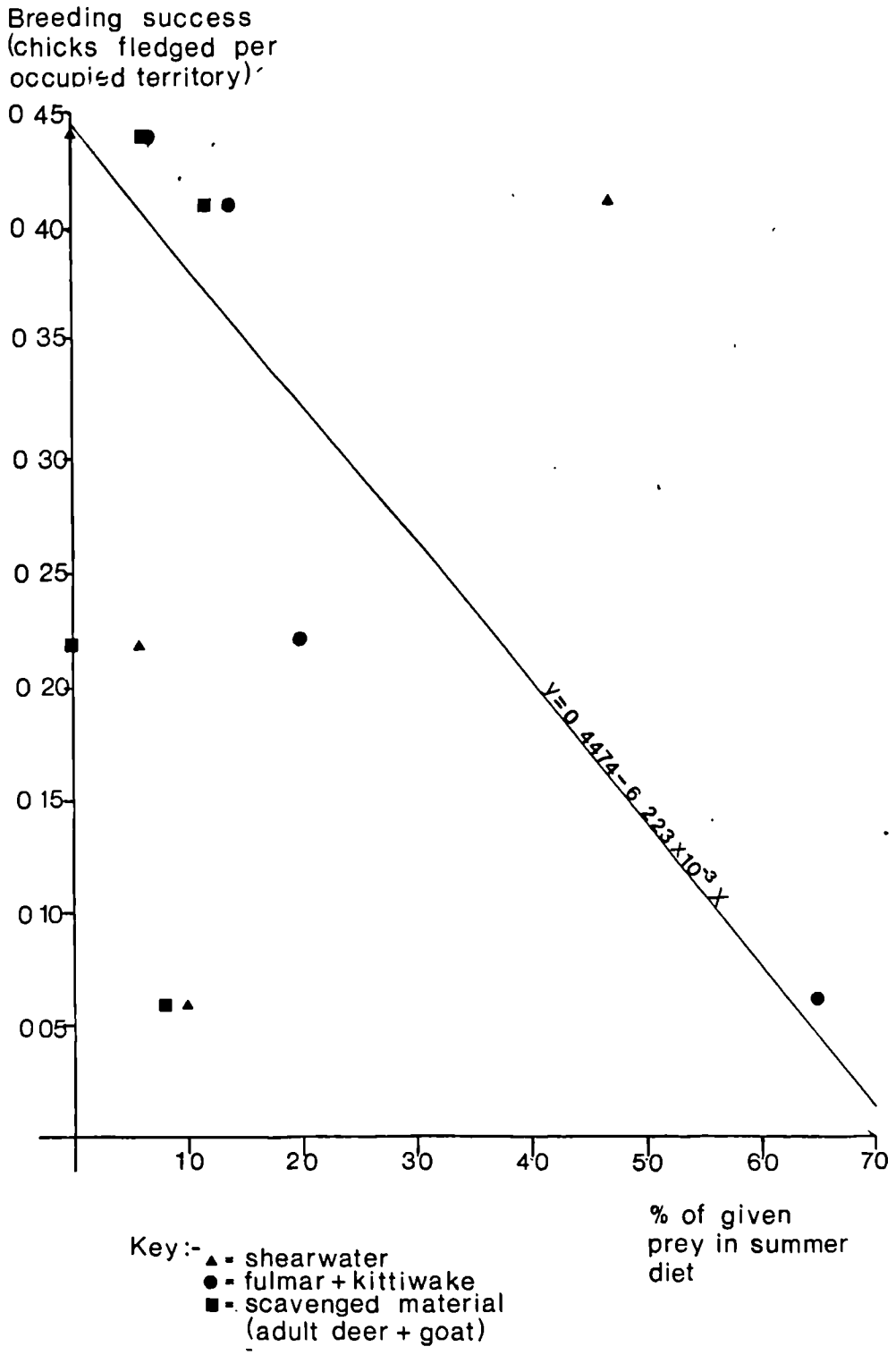
Key to references:-

* Corkhill, 1980
** NCC, unpublished
*** Bourne and Bogan, 1972
† Osborn et al., 1979
†† D. Thompson & R.W. Furness, unpubl.

Notes:-

Values are means for all subjects in each instance

Fig. 6·1 RHUM GOLDEN EAGLE BREEDING SUCCESS IN RELATION TO DIET
(data points are averages over the years 1957-79 for four territories taken from Corkhill, 1980; regression line is of breeding success vs. % fulmar & kittiwake in diet)



derived from seabirds do influence individuals' chances of breeding successfully.

A similar situation appears to exist on Canna where golden eagles' breeding success fell to zero following increased use of fulmars as prey when myxomatosis severely reduced the island's rabbit population (Swann and Ramsey, 1978). Additionally, Ratcliffe (1984) noted that the recovery of peregrine populations in Britain from the organochlorine induced low of the 1960s, has been slower among populations which rely heavily on seabirds than in other areas where terrestrial prey are eaten. That heavy metal contamination may be of more significance to the Rhum population than organochlorines, is suggested by the observation that the sharp increase in PCB levels in eggs between 1978 and 1984 was not coincident with any decline in breeding success. Between 1972 and 1978, 8 young were raised from 24 attempts while from 1979 to 1985, 8 young were raised in 23 attempts (χ^2 = 0.011, df. = 1, $p > 0.10$). Unfortunately no data are available for heavy metal levels in eggs over the same period, so that no firm conclusions may be drawn about the relative impact of the various pollutants taken in by the eagles from their diet.

In conclusion, golden eagle predation of Manx shearwaters on Rhum is not significant to the shearwater population. The extensive use of fulmars and kittiwakes in some eagle territories on Rhum may be depressing breeding success through organochlorine residue or heavy metal acccumulation in the eagles and their eggs. Breeding success of golden eagles on Rhum may also be generally depressed by scarcity of suitable live prey in spring. Further research is required to assess the significance of pollutants to raptors feeding on seabirds.

Great black-backed gulls

In 1985 there were 16 pairs of great black-backed gulls nesting on a stack off the south east coast of Rhum adjacent to the shearwater colony (N.C.C., unpublished records). This species is the major predator of Manx shearwaters on Skokholm and Skomer (Corkhill, 1973). Great black-backed gull prey remains are easily recognised, as the birds turn the skins of their prey inside out. In order to estimate the total shearwater mortality attributable to these gulls, I recorded all gull-handled corpses seen during checks of observation burrows in 1984 and 1985. This is essentially equivalent to a transect count as the same route was consistently followed when checking the burrows. The total length of this route was 260m and all corpses within 10m either side of the line walked were noted giving a total search area of 5200m^2. In 1984 this area was covered on average once in 3.3 days throughout the shearwater breeding season while in the 1985 season the area was covered once every 1.9 days. In each season only 1 gull-handled shearwater corpse was found in the transect. Assuming a total colony area of 311,773m^2 (Wormell, 1976), this leads to an estimate of the toal number of shearwaters eaten by great black-backed gulls each year of:-

$$1 \times (311{,}773 \div 5200) = 60$$

This is clearly a crude estimate, but it is sufficient to indicate the order of the scale of predation involved. That it is a reasonable estimate is suggested by Corkhill's (1973) data for Skomer where a colony of 49 pairs of great black-backed gulls were estimated to take between 270 and 350 shearwaters each year. At the same predation rate, a colony of 16 pairs would take 90 -115 shearwaters annually. In fact, great black-backed gulls on Rhum do not feed exclusively on shearwaters. Of ca 100 pellets collected from the stack in July 1985 and August 1986, less than 5% contained shearwater remains (R.W. Furness, pers. comm.)

In conclusion, consumption of shearwaters on Rhum by great black-backed gulls is probably in the order of 50 -100 birds per year, equivalent to less than 0.05% of the estimated breeding population, and is not detrimental to the shearwater population. Furthermore, many of the shearwaters eaten by these gulls may have been scavenged as gulls have been observed to feed on shearwaters which died through collisions with rocks on landing at the colony (pers. obs.).

Peregrine falcons

Two or three pairs of peregrine falcons hold breeding territories on Rhum each year (N.C.C., unpublished records). Wormell (1965) found shearwater remains at several nests and plucking posts. I have no direct observations of peregrines taking shearwaters, but the regular occurrence of "explosions" of scattered shearwater body feathers within the colony was suggestive of shearwaters being "stooped" upon by peregrines. The incidence of such shearwater remains along the observation burrow check transect described above was 2 in 1984 and 2 in 1985 giving an estimate of 120 shearwaters taken by peregrines each year. Again, this order of predation is not significant to the shearwater population. Even if peregrines using the nest site closest to the shearwater colony were to feed exclusively on shearwaters, at the rate of one bird per day, from April to September less than 200 shearwaters would be taken.

C) Population Dynamics

In order to model the population dynamics of a colony, it is necessary to construct a life table of age-specific fecundity and mortality rates. Ideally, this requires detailed information on the following parameters :-

(1) Fecundity. This is usually expressed as the number of female offspring produced per female per year in each age class.

(2) Recruitment to the breeding population. This is the percentage of offspring which survive to the age of first reproduction and which return to their natal colony to breed.

(3) Adult mortality rate. The percentage of each age class within the breeding population which die each year.

(4) Percentage of non-breeders in the population. The presence of non-breeding adults serves to reduce the average fecundity per head and is therefore of importance to the population model.

(5) Extent of immigration to, and emigration from, the population.

Such detailed information is not available for the Manx shearwater population on Rhum. Indeed, even on Skokholm where many shearwaters are of known age, these parameters cannot be defined for each age class. However, it is possible to construct a useful model of Manx shearwater population dynamics on the basis of existing data by incorporating the following assumptions:-

(1) All females start to breed at the same age.

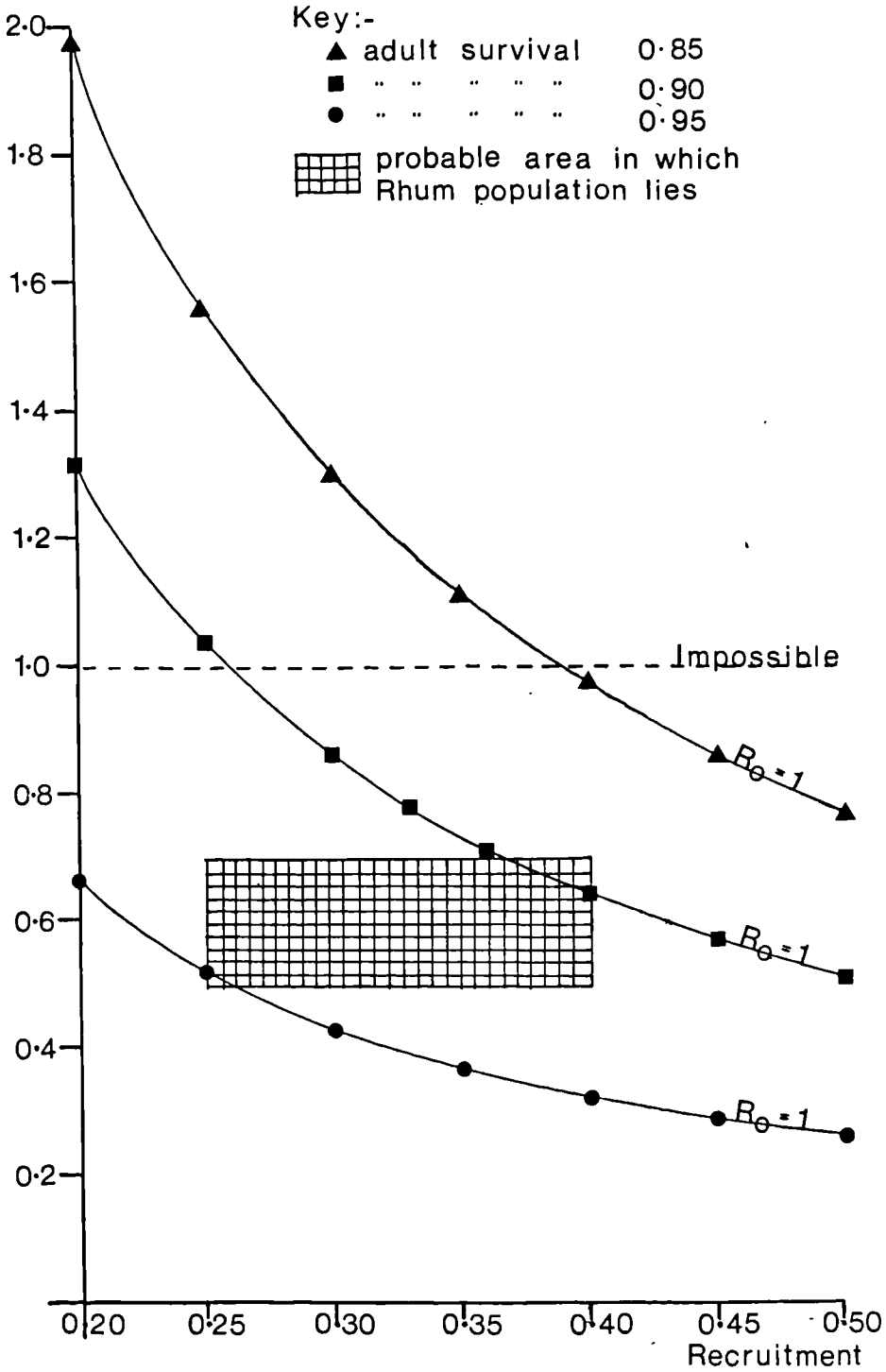
(2) Annual mortality of adults is constant from the age of recruitment to the breeding population.

(3) Female fecundity is constant throughout the reproductive lifespan.

These assumptions do not invalidate the model so long as the values given to the three parameters to which they apply are averages obtained from a random sample of the population which has the same age structure as the population as a whole. This condition has apparently been met in all the reported studies from which I have drawn values for the various demographic parameters used in the population model.

The model is presented in Fig. 6.2. The lines represented are those of zero population growth, which occurs when each female reproduces herself once in her lifetime ie. net reproductive rate, R_o, equals one (Ricklefs, 1973). The model illustrates the dependency of population growth upon adult survival, recruitment and fecundity. In constructing

Fig. 6·2 MODEL OF MANX SHEARWATER POPULATION DYNAMICS



the model, I have taken age of first breeding as 6 years on the basis of Perrins' et al (1973) and Brooke's (1973 and 1977) data for the Skokholm population. In addition, I have assumed that 20% of females of reproductive age do not reproduce in any one year (Brooke, 1977), and that the sex ratio of fledglings is 1:1. Thus, female fecundity is calculated as:-

Fecundity = 0.8 x (chicks fledged per egg laid ÷ 2)

From the model it may be seen that a high adult survival rate is essential to a Manx shearwater population's survival, as it is impossible for fledging success to exceed 1.00. Estimates of average annual adult survival for the Skokholm population have been given as 96% (Harris, 1966a), 90% (Perrins et al, 1973) and 89% (Brooke, 1977). It was not possible to estimate adult survival directly for the Rhum population due to the artificially high rates of burrow desertion caused by over-frequent checking of burrows in 1984 (c.f. Chp. 3). Of 131 known breeders ringed in 1984, only 64% were known to be alive in 1985. If a value of 90% is taken, it can be seen that at an average breeding success of 0.60 on Rhum (mean of P. Wormell's and my own data over 14 years, excluding 1984), recruitment to the breeding population would need to average 0.43 for the population to be maintained. At the average breeding success of 0.70 recorded for Skokholm (Brooke, 1977), a recruitment level of 0.37 would be sufficient to prevent population decline. Recruitment rate is extremely difficult to assess as breeding birds spend little time on the surface of the colony and prebreeders learn to avoid capture (Perrins et al., 1973). Analysis of retrap data for Skokholm led Brooke (1977) to estimate that 25% of fledglings from the colony are recruited to the breeding population. He further concluded that 50% of survivng females emigrate to other colonies to breed and are replaced by an equivalent number of birds from other colonies giving an effective recruitment rate of 4/3 x 25 = 33% (Brooke, 1978b). Results of a thirty year study of a small

population of the demographically similar short-tailed shearwater, suggested that on average 42% of fledglings survive to breeding age (Serventy and Curry, 1984). The mortality rate among Manx shearwaters during the first year of life is apparently much higher than in subsequent years. Harris (1966a) noted that of 141 recoveries of birds ringed as fledglings, 73% were of birds less than four months old, while Perrins et al. (1973) calculated survival rates of prebreeders visiting Skokholm when two or more years old as 86%, only slightly less than that found for adults. The observed correlation between probability of recruitment to the breeding population and fledging weight (cf. Chp. 4) also indicates that the immediate post-fledging period is critical.

The shaded area in Fig. 6.2 indicates the probable area in which the Rhum population lies. The actual growth rate, r, of the colony depends upon the precise values of adult survival and recruitment to the breeding population and upon age of first breeding which affects the generation time, T. Indeed T has a greater influence on r than does net reproductive rate, R_o (Ricklefs, 1973). This model suggests that the existing breeding success rate is probably barely sufficient to maintain the population, and that high recruitment rates are necessary to prevent a decline. It is unknown if recruitment to the Rhum colony is in any way enhanced through net immigration from neighbouring colonies. Population trends on Rhum are now being monitored directly through regular burrow counts and estimates of burrow occupancy within fixed quadrats. The results of this monitoring programme may help to indicate where the Rhum shearwater population lies within the model presented.

The influence of environmental factors upon population size, and possible mechanisms by which the population might be regulated, are discussed in the following chapter.

Chapter 7

DISCUSSION:- POPULATION REGULATION AND LIMITATION

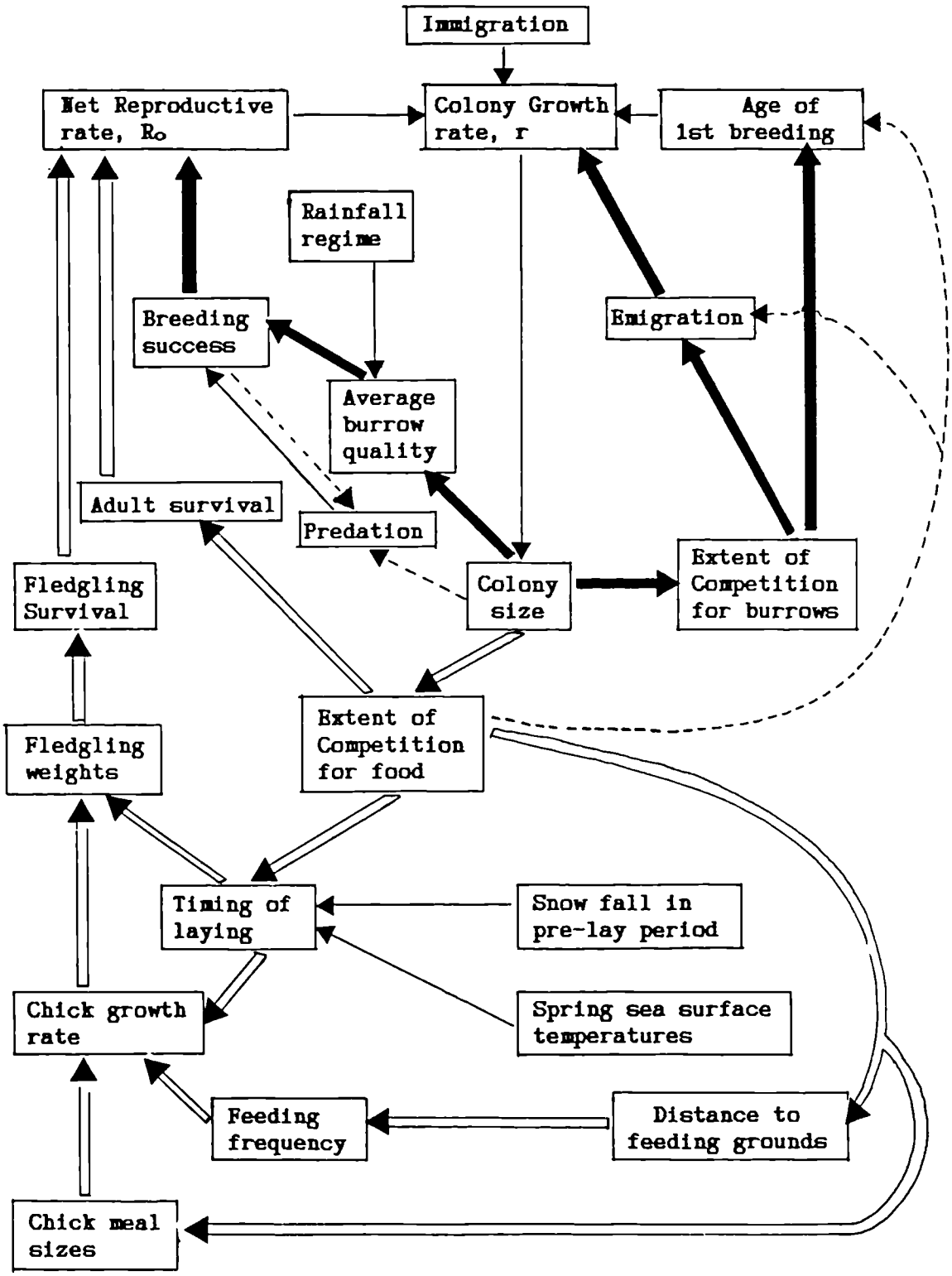
As Ricklefs (1973) has stated, in studying population dynamics it is more important to understand how the population parameters which make up population growth equations vary in relation to environmental factors, rather than merely to assess the mean values of these parameters for a given species. For effective conservation it is essential to be aware of how the demographic equation may alter in response to changes in the physical and biotic environment in which the subject organism lives. Therefore, in this concluding discussion I examine the possible mechanisms by which the Rhum Manx shearwater population may be regulated and from this speculate on which factors may ultimately limit the population's size.

Any discussion of the means by which a population may be regulated, presupposes that regulation does indeed occur. Regulation of seabird populations is generally assumed but is less easily demonstrated (Birkhead and Furness, 1985; Furness and Monaghan, 1987). The degree to which any regulation is density dependent has also been the subject of debate (Andrewartha and Birch, 1954; Lack, 1966), but it is generally held that for vertebrates density dependent factors have a more important influence on population parameters than do density independent factors (Furness and Monaghan, 1987). If density dependence and overall population stability are assumed, the question which then arises is that of which density dependent factor is most important in population regulation:- ie in the maintenance of stability within a given environment. Essentially three main hypotheses concerning density dependent regulation of seabird

populations have been proposed. Lack (1966) considered density dependent mortality outside the breeding season to be the key factor. Among tropical seabirds, Ashmole (1963) also considered density dependent competition for food supplies to be the key factor, but considered that competition for food would be greatest during the breeding season. He argued that breeding birds are restricted in their potential foraging range by the need to visit the breeding colony and are also subject to higher energetic demands when rearing young than at other times. This type of regulation could also apply to seabirds breeding at higher latitudes in instances where the seasonal improvement in food abundance or availability during the breeding period is insufficient to compensate for the increased food requirement and restriction in foraging range associated with the same period. Regulation by availability of nest sites has generally been considered to be exceptional (Birkhead and Furness, 1985). Regulation of this type could occur in instances where the size and reproductive success of the breeding population is so limited by lack of nest sites that recruitment is reduced to the level at which it balances annual adult mortality at a population density lower than that at which food supply becomes a regulatory factor.

In considering the relative importance of various density dependent factors to the Manx shearwater population on Rhum, it is useful to examine a simple model of the potential regulatory mechanisms. This is presented in Fig. 7.1. Essentially there are two possible mechanisms of density dependent regulation of the population. Routes by which competition for burrows might promote population stability are indicated by solid arrows, while routes by which the population might be regulated as a result of competition for food supplies are shown by open arrows. Single line arrows indicate effects which are pertinent regardless of the actual mechanism of regulation. Broken arrows are used where a relationship is uncertain.

Fig. 7.1 Possible mechanisms of density dependent regulation of the Manx shearwater population on Rhum.



The results presented in this thesis indicate that the number of fledglings produced and surviving to recruitment is determined by two main factors. The first is the breeding success rate, defined as the number of fledglings produced per egg laid. The results presented in Chapter 3 indicate that breeding success varies mainly according to hatching success which is itself significantly influenced by rainfall and burrow quality. The demonstrated variability in burrow quality in the Rhum shearwater colony suggests that colony breeding success may be density dependent due to the decrease in average burrow quality with increasing colony size. This is analogous to the situation in the Farne Islands shag colony described by Potts et al. (1980). Increased competition for burrows may also influence colony growth rate if young birds are unable to obtain nest sites. Brooke (1977) found evidence that age of first breeding on Skokholm had increased as the colony grew. He was unable to determine whether competition for burrows or for food resources was responsible for this effect. However, a change in age of first breeding is unlikely to have such an immediate and direct effect on colony growth as would the decline in breeding success with fall in average burrow quality on Rhum where hatching success in the 50% upper quality burrows was over twice that in the lower 50% (cf. Table 3.6). A reduction in breeding success caused by the lowering of average burrow quality might be further re - inforced through increased potential for rats to overwinter in the colony and act as predators during the breeding season as apparently occurred on Canna in 1982 (Swann, pers. comm.). However, the reduction in average breeding success which would probably be required for this to occur would be unlikely within the proposed regulatory system, as lag time between population increase and subsequent decrease would be relatively short.

As discussed in Chapter 4, weight at fledging influences post-fledging survival, probably due to the

requirement for young to undertake long distance migration immediately after leaving their natal colony. Timing of breeding has a significant effect on fledging weights with later hatched chicks growing more slowly and delaying fledging. Increased competition for food might influence fledging weights in two ways. Increased competition for food during the pre-laying period might result in females taking longer to form their eggs thus delaying mean laying date. Greater competition for food during the chick rearing period might reduce the average amount of food caught by individuals during each foraging trip or force increasing numbers of birds to forage further from the colony. Hunt et al. (1986) have demonstrated that auk chicks at a large mixed colony in the Pribilof Islands had lower growth rates and fledging weights than those from a smaller colony in the same area. They suggested that greater feeding interference between individuals at the larger colony might be responsible for the observed effects of colony size on chick growth. However, the relative sizes of the two colonies examined were 10 : 1. Clearly, for food supply to act as a regulatory factor much lesser alterations in colony size would need to cause similar, if less marked, effects.

Brooke (1977) concluded that he was unable to assess the relative importance of competition for food and nesting burrows to the population dynamics of the Skokholm population. He did not investigate the possibility of there being significant variability in burrow quality, but burrow flooding is not mentioned as occurring in the Skokholm colony in any of the papers pertaining to it which I have seen. It may be that the marked variation in nest site quality observed in the Rhum colony is unusual. It is clearly a function of the very high rainfall within the colony. This begs the question as to why the colony was established in such a wet area. There are several possible explanations including the suitability of the substrate for burrow excavation and the opportunity for avian predator avoidance

offered by the steep slopes and frequent low cloud or mist (Storey, 1986). The evidence presented in Chapter 6 also suggests that if the colony were closer to the coast, or occupied a greater area extending nearer to the coast, it might be subject to rat predation.

Since the effects of fledging weight on future survival can only operate if any fledglings are produced in the first place, I suggest that the most plausible mechanism by which the Rhum shearwater colony might be regulated is through density dependence of average burrow quality and hence breeding success. Birkhead and Furness (1985) demonstrated that population regulation through density dependence of nest site quality is less feasible for strongly K-selected seabirds such as fulmars than for inshore feeders such as shags which have relatively high reproductive rates. However, the following hypothetical example suggests that regulation of shearwaters on Rhum by this mechanism is feasible:-

Consider a stable population of 666 pairs of shearwaters nesting in a colony where there are the following burrows:-

100	in	which	breeding	success is 0.8
200	"	"	"	" 0.6
300	"	"	"	" 0.4
400	"	"	"	" 0.2

Rate of recruitment of fledglings to the breeding population is assumed to be 0.4 and annual adult survival is 0.9.

Note that:-

a) The average quality (ie. breeding success rate) of the upper quality 500 burrows is 0.56 and that of the lower 500 burrows is 0.24 ie the breeding success rate in the top 50% of burrows is just over twice that in the lower 50%.

b) At the stable population level of 666 pairs, overall colony chick production per year is 333 equivalent to 0.50 chicks per pair.

Thus this hypothetical colony is similar in basic population parameters to that on Rhum.

The table below illustrates the balance between recruitment and mortality at a variety of population levels in the hypothetical population described above.

Breeding pairs	No. chicks fledged	Recruitment (R)	Mortality (M)	R-M
500	280	112	100	12
550	300	120	110	10
600	320	128	120	8
620	324	130	124	6
640	328	131	128	3
660	332	133	132	1
680	336	134	136	- 2
700	340	136	140	- 4
750	350	140	150	-10
800	360	144	160	-16

This simple model suggests that population regulation through density dependent breeding success mediated by burrow quality is possible for a population of Manx shearwaters such as occurs on Rhum.

So far, this discussion has concentrated on the possible mechanisms by which a stable population of shearwaters on Rhum might be regulated. At the moment it is unknown if the population is in fact stable and this leads to the question of the effects which changes in environmental factors might have on the population. Factors affecting either the ability of adults to hatch eggs or to provision chicks may limit the population size. In the former instance it might be hypothesised that a major alteration in Rhum's rainfall regime might alter the colony's potential size by effectively increasing or decreasing the average quality of all burrows (ie. occupied or not) in the colony. For

example, in the hypothetical colony described above, an increase in rainfall which had the effect of reducing mean breeding success in all burrows by 0.1 would reduce the population level at which annual recruitment balances mortality to 400 pairs. Alternatively, any alteration in overall food abundance or its temporal or spatial availability and predictability could adjust potential colony size. If, in the example above, a reduction in mean fledging weight caused survival to breeding age to fall to 0.35 population size would stabilise at only 460 pairs. Such changes could occur directly eg through Man's fishing activities, or indirectly due to climatic change altering the timing and/or extent of the seasonal rise in marine productivity. Increased availability of food resulting from Man's fishing activities has been postulated as being responsible for the dramatic increase in the North Atlantic fulmar population over the past century (Fisher, 1952).

This discussion leads to several recommendations for the future conservation management of the Rhum shearwater colony:-

1) The permanent plots established by R.W. Furness in 1985/6 should continue to be monitored at regular intervals of five years or less, so that any major population trends may be detected. Ideally, this work should be carried out during the early part of the incubation period prior to the main mortality of eggs and before large numbers of non-breeding birds are occupying burrows.

2) Thirty or more of the existing observation burrows should be checked each year in the early incubation period, early chick period and late chick period to provide hatching and fledging success information. In the event of any major failure in breeding success being indicated by these checks, the level and persistence of rat activity in the colony should be monitored throughout the following twelve months by means of regular transect counts of droppings, snow tracks and any other rat signs. In the event of rats remaining in

the colony at detectable densities throughout the year, any attempt at a control campaign should be carried out in early spring when the population should be at a minimum. The use of poison bait would be most effective if placed in the entrances of burrows which snow tracks and/or droppings indicated to be occupied by rats. However, as stated in Chapter 6, I feel that it is unlikely that a damaging rat population could become established in the shearwater colony, because of its location, unless the shearwaters suffered major breeding failures over several consecutive years.

3) At the moment there is no information on the extent of interchange of birds between Rhum and other breeding colonies. It would be useful to gain some indication of the extent to which the Rhum colony is dependent upon its own reproductive output for population maintenance. To this end continued ringing of Rhum fledglings is desirable. The ring numbers of any ringed birds observed in the colony should also be noted and checked to determine the origins of these birds.

4) If the colony is currently limited in size by the average quality of burrow, as dictated by the existing rainfall regime, the large scale provision of flooding resistant artificial burrows within the colony might serve to increase the colony size through improved breeding success. This is unlikely to be practical, but the small scale experimental provision of such burrows begun by R.W. Furness, with Earthwatch volunteers, in 1986 should provide useful insights into the extent of existing competition for burrows within the colony.

In this thesis I have attempted to unravel some of the complexities of the Rhum Manx shearwater population. It was not possible to examine any of the intrinsic, age or breeding experience related factors, influencing reproductive success or mortality. Brooke's (1977) results from Skokholm indicated that whereas breeding experience influenced hatching success, inherent variations in bird "quality"

rather than age or experience were involved in determining individuals' timing of breeding, egg volume and chick fledging weights. The results of this study highlight burrow quality as being important to reproductive potential, but the extent to which bird quality and burrow quality are linked is as yet unclear. Investigation of the influence of food availability on the colony's population dynamics would have required detailed monitoring of prey stocks and assessment of local prey depletion. Such studies were beyond the scope of this thesis, but my results do indicate that food availability varies both within and between seasons, and that it influences several aspects of reproductive performance.

SUMMARY

1) Manx shearwaters are believed to have bred on Rhum for at least nine centuries, and the colony is currently the species's largest. The main aim of this study was to investigate the influence of extrinsic factors such as predators, habitat, diet and climate upon the breeding biology and population dynamics of the Rhum Manx shearwaters. This information will be helpful in formulating management policies to ensure the conservation of the colony. Fieldwork for the study was undertaken during the 1984, 1985 and 1986 breeding seasons.

2) Male shearwaters on Rhum are larger and heavier than females. Head length and the ratio of wing length to bill length were the best two of the parameters measured for discriminating between the sexes:- 76.7% of birds were correctly classified by the discriminant function derived from these variables.

3) Males on Rhum are larger than those from the Skokholm colony in Pembrokeshire. Female shearwaters on Rhum also tend to be larger than those on Skokholm, but the difference is less marked, possibly as a consequence of the greater tendency for females to disperse from their natal colonies.

4) Paired birds are generally lighter during the pre-laying period than later in the breeding season. Successfully breeding birds maintain fairly constant weights from laying to the end of the chick rearing period whereas failed breeders decline in weight after incubation.

5) During the pre-laying period paired birds on Rhum are generally lighter than those on Skokholm, despite their greater size, and may experience a relative food shortage at this time.

6) In 1984, hatching success was significantly reduced in those burrows where the incubating adults were most frequently disturbed by the observer. In 1985 and 1986,

breeding adults were not handled during incubation and hatching success rates were 52% and 75% respectively.

7)

a) Hatching success on Rhum is significantly negatively correlated with the number of days experiencing unusually heavy rain during the incubation period. This results from the flooding of greater numbers of burrows in wetter years.

b) Survival of chicks from hatching to fledging is consistently high (84 - 85% during the current study), and is not influenced by the amount or distribution of rainfall during the chick rearing period.

Thus, a major determinant of overall colony breeding success each season is the incidence of heavy rain during the incubation period.

8)

a) Breeding burrows vary, according to their topography, in their susceptibility to flooding during heavy rain. Flooding susceptibility of individual burrows may be assessed on the basis of ground slope and depth to give a non-linear index of burrow quality.

b) Eggs are both more likely to be laid, and more likely to hatch, in those burrows least susceptible to flooding ie. breeding success is greater in higher quality burrows. In 1984 and 1985 hatching success in burrows of greater than average quality was more than twice that in burrows of less than average quality.

These results lead to the conclusion that, in the absence of any large scale immigration from other colonies, the size of the shearwater breeding population on Rhum may ultimately be limited by the availability of good quality nest sites.

9)

a) Wing length is apparently indicative of bird quality as it is significantly positively correlated with weight per unit body size. In 1985, there was a significant tendency for longer winged males to occupy better quality burrows. This suggests that there may be competiton between males for

occupancy of good quality burrows with the result of better quality birds holding better quality nest sites.

b) Male birds are more likely to change burrows from one year to the next following breeding failure than breeding success. Female movement between burrows from year to year is not apparently related to breeding success.

c) Shearwaters on Rhum are apparently unable to assess burrow quality other than by attempting to breed in a given burrow.

It appears that male shearwaters on Rhum tend eventually to occupy good quality burrows through a trial and error process of attempting to breed in available burrows until consistently successful in one nest site. Individual bird quality may limit ability to occupy the best quality burrows. This would tend to lead to the best burrows being occupied by the most experienced and/or best quality breeders. Thus, in addition to the direct effect of burrow quality on breeding success caused by susceptibility to flooding, there may also be an indirect effect due to more proficient breeders occupying better quality burrows.

10)

a) On Rhum, as on Skokholm, chick weight at fledging declines seasonally. On Skokholm, post fledging survival has been found to be positively correlated with weight at fledging. On the basis of calculations of potential migratory flight ranges, it would appear that it is feasible for Rhum fledglings of average weight to migrate directly to South America without needing to feed en route. Lighter than average birds may be forced to find food en route if they are to survive and complete the migration.

b) On Rhum, later hatching chicks tend to fledge older than early chicks, but there is no significant correlation between peak chick weight and hatching date. This suggests that the seasonal decline in fledging weights arises from difficulties experienced by adult shearwaters in provisioning their young late in the season.

These observations indicate that there is a selective advantage in breeding as early as possible

11)

a) Prolonged snow cover at higher altitudes in the colony may delay occupation of burrows in these areas at the start of the breeding season and lead to later laying due to a delay in commencement of the "honeymoon" period.

b) In both 1984 and 1985 the median laying date on Rhum was 12th May but in 1986 it was significantly later on 21st May. This delay in laying in 1986 was coincident with significantly reduced air temperatures and increased frequency of strong winds in the spring. Both of these factors may influence marine food abundance and availability to shearwaters.

c) Breeding shearwaters on Rhum feed predominantly on a mixture of small squid, particularly juvenile Ommastrephidae, and fish up to 80mm long, including sandeel and sprats/herring. The proportion of fish in the diet apparently increases from the pre-laying to chick-rearing period.

d) Incubation period was not correlated with laying date which suggests that earlier layers do not experience any increased difficulty in incubating eggs. This implies that once food supplies are sufficient to enable females to form eggs, they will not constrain successful incubation.

e) There is no general correlation between female size and laying date.

f) The energetic requirements of egg formation are apparently considerably less than those of successful incubation, which suggests that the latter may ultimately have determined the laying date of shearwaters on Rhum. Proximate control of laying may be exerted through a requirement for calcium rich foods for eggshell formation.

12)

a) Egg volume increased significantly with laying date in 1985 and 1986, possibly as a result of spring weather

conditions in these years preventing some birds from forming eggs until feeding conditions were relatively good. In 1986 there was some indication of inexperienced breeders laying relatively large eggs late in the laying period. There was no seasonal trend in egg volume in 1984.

b) No significant correlation was observed between egg volume or weight and female body dimensions or condition.

c) Larger and heavier eggs tended to produce larger and heavier chicks at hatching, but there was no correlation between fledging weight and egg size.

From the above, it appears that timing of breeding has a greater influence on breeding success than does the size of egg laid. Laying date may be influenced by females' ability to find appropriate calcium-rich food during egg formation. Egg volume may be less dependent upon the foraging ability of individuals as the process of albumen formation appears to be relatively undemanding.

13)

a) Average growth rates of chicks were significantly lower in 1985 than in 1984.

b) In both 1984 and 1985 chick growth rate was significantly negatively correlated with hatching date.

14)

a) There was no significant difference in the average size of feed delivered to chicks in 1984 (75.4g) and 1985 (69.5g). Feeding frequency was, however, significantly greater in 1984 than in 1985 with mean intervals between feeds of 1.18 and 1.34 days respectively.

b) In 1984, chicks were fed larger meals during the middle phase of their growth (31 - 55 days old) than when younger or older, but in 1985 feed size did not vary significantly with age. In 1984, chicks were fed more frequently when between 41 and 55 days old than at other times.

15) Food conversion efficiency in 1984 averaged $0.58 gg^{-1}$. Chicks on average required a 69g feed to maintain body weight

from day to day. Food conversion efficiency declined with increasing chick age.

16)

a) Brown rats on Rhum were not active predators of Manx shearwaters or their eggs and young in the course of this study.

b) A small, possibly migratory, population of rats scavenges within the shearwater colony particularly during the autumn and early winter.

c) The location and habitat of the existing shearwater colony on Rhum apparently prevents a damaging rat population from becoming established within the colony.

17) Predation of shearwaters on Rhum by golden eagles, great black-backed gulls and peregrine falcons is not significant to the shearwater population.

18) The poor breeding success of golden eagles on Rhum may result from a lack of live prey in their diet combined with accumulation of toxins from seabirds taken as prey.

19) It was not possible in the course of this study, to assess whether the Rhum shearwater population is stable, in decline or increasing. At the levels of breeding success recorded, a recruitment rate of ca. 0.4 fledglings surviving to breeding age is apparently necessary to sustain the colony. It seems likely that burrow quality on Rhum is the single most important factor currently limiting population numbers.

Appendix 1

NAVIGATION TO THE BURROW

Introduction

The question of how nocturnal, burrow-nesting birds locate their nests in large colonies has been the subject of some debate. Essentially there are four possiblilities:-

1) Members of pairs recognise each other's calls and can therefore locate the correct burrow by homing in on the calls of their mate in the burrow. Brooke (1978d) found that male and female shearwater calls are distinct and that individual females can recognise their own mates. However, there was no indication of male recognition of individual females' calls. In addition, James (1985) found that most calling was by prospecting immatures rather than breeding adults. His results suggested that calling has a dual role in territorial defence and sexual advertisement. As breeding males are capable of relocating their previous season's burrow prior to the return of their mates, and both sexes return alone to silent burrows during chick rearing, there is little evidence to support the theory of homing through mate call recognition.

2) Manx shearwaters use echo-location to locate their burrows. This was first suggested by Lockley (1969). Brooke (1978e) pointed out that the audible calls of Manx shearwaters are completely unlike those used by various cave-nesting species which are known to use echolocation. The possibility that ultrasonic signals could be used has yet to be investigated.

3) Manx shearwaters locate their burrows by visual reference to landmarks in the colony. Brooke (1978e) tested this possibility experimentally by providing distinctive visual cues, in the form of white boxes, at burrow entrances.

The test group of boxes were then moved short distances to the side and fitted with traps to discover if incoming birds were confused by the change in position of the visual cue. The results were not entirely conclusive as less than 30% of the test birds failed to relocate their burrows following the change in position of the cue, but they did suggest that vision may play at least some part in burrow location.

4) The observation that petrels and shearwaters appear to have a highly developed olfactory sense in comparison with most other birds (Bang and Cobb, 1968), has led to the suggestion that this may be used in navigating to breeding colonies or even individual nest sites. The use of smell in locating food at sea has been experimentally demonstrated for several species (Hutchison et al., 1984; Grubb, 1972). Grubb (1974) investigated the possibility that Leach's petrels nesting under coniferous forests in New Brunswick might use olfactory guidance to their burrows. Observations of the birds' approach behaviour to their burrows and tests of the homing ability of birds which had been operated on to destroy their sense of smell suggested that these petrels might indeed use olfactory cues in navigating to their nests. However, the experimental destruction of the sense of smell might in any case have reduce rates of return to the burrows by making it difficult for the birds to locate food. Grubb (1974) also used an olfaction choice chamber to test the birds' ability to discriminate between their own nest material and forest floor leaf litter. The results of this did suggest that Leach's petrels were capable of distinguishing between nest material and leaf litter on the basis of odour. The experiment did not however test the birds' ability to discriminate between their own nests and those of other Leach's petrels. Shallenberger (1975) tested the respiratory responses of wedge-tailed shearwaters to exposure to odours from their own versus other nest material. He found no consistent indication that the birds tested recognised their own nest odours.

Methods

In order to examine the possibility that Manx shearwaters on Rhum might use olfactory cues to recognise their burrows I used a simple T maze. The maze was constructed of metal sheeting lined with black felt. The test material was placed on cardboard trays in two artificial nest chambers situated at the end of each arm of the T. Four treadle switches, two placed half way along each arm of the maze and the other two just outside the artificial nest chambers, triggered microswitches when depressed and so produced a trace on a four track chart recorder. The maze was situated in a quiet, darkened room and the test birds were left in it for periods of 6 to 8 hours at a time during trials. Their movements within the maze were followed retrospectively by reference to the recorder traces.

The maze trials were carried out in July and August 1986. The six birds used were paired adults from three observation burrows where nests had been built but in which either no egg had been laid (2 cases) or the egg had failed to hatch. A total of 27 trials were conducted, between 3 and 7 on each bird. No bird was subject to more than 4 trials, or kept for more than 72 hours, at any one time. In 5 cases the choice was between the bird's own nest and an empty chamber, in 19 instances it was between the bird's own nest material and that from a different nest and in 3 instances between the bird's own nest and fresh grass and moss such as the Rhum shearwaters use to build nests. The birds' nests were stored in polythene bags between trials and were allocated randomly to either the right or left chamber in each instance. They were always moved together with the cardboard tray on which they had originally been placed to prevent the odour of any one nest becoming established in either chamber. The entire maze was swept out between trials to remove remnants of nest material from the tunnels and chambers.

Results and Conclusions

In 5 of the 27 trials, the test bird remained in the maze entrance tunnel throughout. A choice was defined as having been made when the bird entered one or other of the maze chambers. Only the first choice in each trial was used in further analysis. The results are shown in Table A.1. O values are observed frequencies and E values expected frequencies.

Table A.1 Chi^2 analysis of nest chamber choice in the T maze trials.

a) Choice of own nest versus other nest, empty chamber or fresh nest material.

Choice made	Own nest in right-hand chamber	Own nest in left-hand chamber	Totals
Own nest	O = 6 E = 4.1	O = 4 E = 5.9	10
Other nest etc.	O = 3 E = 4.9	O = 9 E = 7.1	12
Totals	9	13	22

$\chi^2 = 1.506$, d.f. = 1, N.S.

b) Choice of right-hand versus left-hand chamber.

Choice made	Own nest in right-hand chamber	Own nest in left-hand chamber	Totals
Right-hand chamber	O = 6 E = 6.1	O = 9 E = 8.9	15
Left-hand chamber	O = 3 E = 2.9	O = 4 E = 4.1	7
Totals	9	13	22

$\chi^2 = 0.114$, d.f. = 1, N.S.

The same results are presented in two different formats to illustrate the two main conclusions which may be drawn from them ie.

1) The birds showed no significant tendency to choose their own nest material in preference to an empty chamber, fresh material or another nest.

2) The birds showed a significant preference for the right-hand chamber (chosen on 68% of all trials as compared with the 50% expected if movement was purely random, $Z = 1.745$, $p < 0.05$, for angularly transformed proportions) regardless of which chamber contained their own nest material. I have no satisfactory explanation for this observed preference of the birds for the right-hand chamber. It is of interest to note, however, that in all three burrows from which the test birds were taken, the nest chamber lay to the right of the burrow entrance.

In conclusion, the results of this experiment provide no evidence of olfactory guidance to the nest burrow among Manx shearwaters on Rhum. However, they do not prove that this does not occur. The stress imposed on the birds by being placed in such artificial surroundings, the small sample of individuals used and the unexplained bias to one side of the choice chamber all limit the validity of attempting to draw any general conclusions from the results of this experiment. However, several general observations lead me to believe that Manx shearwaters on Rhum most probably use visual cues in navigating to their burrows. The colony site is littered with boulders of distinctive shapes and sizes which are of considerable use to the human observer in navigating successfully around the colony both by day and at night (pers. obs.). Grant and Nettleship (1971) similarly hypothesised that puffins nesting in Iceland might use boulders as landmarks to help them to land as close as possible to their burrows and so minimise the risk of predation. In addition, male shearwaters returning to Rhum

successfully relocate burrow entrances hidden under several inches of snow. At this time, the ground in the colony remains frozen to a depth of several centimeters (pers. obs.). These conditions would tend to minimise any distinctive odours originating from the previous season's nest material. Similarly, Manx shearwaters are capable of re-excavating burrows which have had their entrances blocked by earth or rocks which would also tend to reduce the strength of any olfactory cues present (pers. obs:- 7 of 16 burrows blocked in 1985 re-excavated in 1986; Brooke, 1977). Further experiments, involving the manipulation of both visual and olfactory cues available to the shearwaters, are required to assess the relative importance of vision and olfaction to Manx shearwaters in navigating to their burrows.

Appendix 2

SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

Herring	*Clupea harengus*
Sprat	*Sprattus sprattus*
Sheppy argentine	*Maurolicus sp.*
Sandeel	*Ammodytes* spp
Jackass penguin	*Spheniscus demersus*
Wandering albatross	*Diomedea exulans*
Royal albatross	*Diomedea epomophora*
Fulmar	*Fulmar glacialis*
Antarctic petrel	*Thalassoica antarctica*
Grey-faced petrel	*Pterodroma macroptera gouldii*
Phoenix petrel	*Pterodroma alba*
Great shearwater	*Puffinus gravis*
Wedge-tailed shearwater	*Puffinus pacificus*
Sooty shearwater	*Puffinus griseus*
Slender-billed or short-tailed shearwater	*Puffinus tenuirostris*
Christmas shearwater	*Puffinus nativitatus*
Manx shearwater	*Puffinus puffinus*
Hutton's shearwater	*Puffinus huttoni*
Newell's shearwater	*Puffinus (auricularis) newelli*
Audubon's shearwater	*Puffinus l'herminieri*
Leach's storm-petrel	*Oceanodroma leucorhoa*
Fork-tailed storm-petrel	*Oceanodroma furcata*
South -Georgian diving petrel	*Pelecanoides georgicus*
Gannet	*Sula bassana*
Shag	*Phalacrocorax aristotelis*
Golden eagle	*Aquila chrysaetos*
Peregrine falcon	*Falco peregrinus*
Red grouse	*Lagopus lagopus scoticus*
Ptarmigan	*Lagopus mutus*
Great skua	*Catharacta skua*
Lesser black-back gull	*Larsus fuscus*
Great black-back gull	*Larus marinus*
Kittiwake	*Rissa tridactyla*
Common tern	*Sterna hirundo*
Roseate tern	*Sterna dougallii*
Black skimmer	*Rynchops niger*
Razorbill	*Alca torda*
Brunnich's guillemot	*Uria lomvia*
Common guillemot	*Uria aalge*
Black guillemot	*Cepphus grylle*
Ancient murrelet	*Synthliboramphus antiquum*
Cassin's auklet	*Ptychoramphus aleuticus*
Least auklet	*Aethia pusilla*

Rhinocerous auklet	*Cerorhinea monocerata*
Atlantic puffin	*Fratercula arctica*
Cuckoo	*Cuculus canorus*
Eastern kingbird	*Tyrannus tyrannus*
Great tit	*Parus major*
Hooded crow	*Corvus corone*
Red-billed quelea	*Quelea quelea*
Mountain hare	*Lepus timidus*
Rabbit	*Oryctolagus cuniculus*
Field mouse	*Apodemus sylvaticus*
Brown rat	*Rattus norvegicus*
Ship or black rat	*Rattus rattus*
Polynesian rat or kiore	*Rattus exulans*
Red deer	*Cervus elaphus*
Feral goat	*Capra liscus*

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